ANTI-PREDATOR TRAINING: AN EXPERIMENTAL APPROACH IN REINTRODUCTION BIOLOGY

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by

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"Curiouser and curiouser....."

Alice in Wonderland,
Lewis Carroll, 1961.

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ABSTRACT

Captive-rearing of animals for reintroduction into the wild not only involves propagation of individuals, but should also be concerned with ensuring that animals destined for release have the skills necessary to thrive in the wild. In recent years greater attention as been dedicated to preparing captive-reared individuals for life post-release. Predation is a major cause of mortality of reintroduced animals, but techniques to prepare captive-reared animals to cope with predators are often perceived to be difficult to design and implement.

Here I show results of attempts to condition the black stilt (*Himantopus novaezealandiae*), a critically endangered wading bird species, to be wary of cats. Annually, about 30 black stilts are raised in captivity for release into the wild. A major source of post-release mortality is thought to be mammalian predators. The ability of juvenile captive-reared black stilts to recognise and learn to be wary of the cat (*Felis catus*), was studied in two experiments conducted between November 1992 and August 1994.

Cats are not historical enemies of black stilts as mammalian predators are a relatively new introduction to New Zealand (in the last 100 years). However, captive-reared juvenile black stilts responded cautiously to the cat model upon their first encounter, suggesting some genetic recognition of mammalian predators already existed. Antipredator-training by conditioning involved structured presentations of a moving cat model (conditioned stimulus) paired with alarm calls (unconditioned stimulus), and was conducted at various ages. In Experiment I, two thirds of the birds received antipredator-training and one third did not. Few differences were found between antipredator responses of the two groups, and post-release survival was the same for trained and untrained birds. In Experiment II recognition of cat and control models by juveniles that had been anti-predator trained at different ages was investigated. Results indicated that captive-reared black stilt juveniles were capable of learning to be more wary of cats after training, although some decrement of predator recognition behaviour occured over time, possibly due to factors such as habituation and extinction of responding.

I suggest that conditioning captive-reared animals about predators is a valuable addition to existing reintroduction programmes, and make suggestions for efficient introduction of antipredator-training into the current black stilt management programme.

Chapter 1
INTRODUCTION

1.1 Captive-rearing and reintroduction: a way to conserve species.

With the continuing encroachment of human activities on natural habitats, numerous species are in danger of extinction. In an effort to conserve species, government and private organizations frequently initiate captive-rearing programmes, where the ultimate goal is often reintroduction of captive-reared individuals into the wild. Reintroduction involves the movement of captive-raised animals into or near their species' historical range to re-establish or augment a wild population (Beck et al. 1994). With the proliferation of captive-breeding and release programmes (see Beck et al. 1994), it has become increasingly obvious that most captive-rearing facilities do not provide the opportunities for animals to develop necessary skills to maximise their chances of survival upon reintroduction into the wild. For example, wild-reared Siberian polecats (*Mustela eversmanni*, Miller et al. 1994) and golden lion tamarins (*Leontopithecus rosalia*, Beck et al. 1991) survived longer and adapted quicker than captive-reared animals reintroduced at the same sites, suggesting that captive-reared animals may have inferior survival skills to those reared in the wild. If captive-reared animals can be given experiences closer to wild-reared animals, they should survive better.

1.2 Skill acquisition and development in the captive environment.

All complex behaviour patterns, including survival skills, develop as a result of extensive interaction between innate responses due to genetics (Curio 1975; Coss & Owings 1978; Magurran 1990) and an animal's experience (Stefanski & Falls 1972; Polsky 1975; Curio et al. 1978; Conover 1987; Seyfarth & Cheney 1990), so survival skills should improve and develop with practice. Animals need to be given as natural or complex a rearing environment as possible, to allow the animals to build on their

innate abilities (McLean & Rhodes 1991; Kleiman 1989).

In the wild, reintroduced animals need to forage effectively, find refuge, breed, and avoid predators. Captive environments are commonly very different from the natural habitat in terms of space, diet, exposure to disease, complexity of social relations, mate choice and predator-prey interactions (Mason 1986 cited in Box 1991), and therefore may not permit animals to refine whatever instinctive survival skills they possess with practice. Additionally, some captive-rearing programmes involve hand-raising animals in isolation from their parents. Young birds learn a number of skills from their parents (Hamilton 1975; Sordahl 1980; Stamps 1991), and animals raised without parents may have difficulties finding food and shelter and learning about general concepts such as wariness.

As captive environments do not truly represent natural situations, individuals born in captivity may never exhibit a full range of potential natural behaviours (Box 1991). Two interrelated factors are likely to influence post-release survival of reintroduced animals: First, the capacity to learn new and flexible behavioural skills in response to a new, dynamic environment; and second, the possession of specific survival skills gained from previous experience. Both of these factors may be influenced by the quality of the pre-release environment. A useful question to ask for captive breeding and reintroduction programmes is *how* the quality of the captive environment can be improved. Specifically, which behaviours of the animal should be encouraged and how this can be done. Many of the behavioural skills and strategies necessary for survival are not genetically fixed (Box 1991); therefore, species managers could potentially augment the skills animals gain in the captive environment through environmental enrichment and behavioural training regimes. It has be shown that environmental enrichment can enhance natural behaviours of several captive-bred species (Box 1991). For example, spatial co-ordination and locomotion of golden lion tamarins can be improved by providing complex activity areas, improving the ability of captive-released individuals to move around natural vegetation (Redshaw & Mallinson 1991). In a review of global reintroduction practices since 1900, Beck et al. (1994) found that reintroduction programmes that were deemed successful used pre-release training more often than did unsuccessful release efforts.

1.3 Reintroduced animals coping with predators in the wild environment.

It is widely accepted that vertebrate predators typically capture higher than expected proportions of substandard individuals from prey populations (e.g., Curio 1976; Morse 1980). Individuals that are especially vulnerable are the young, weak, sick, aged, injured and inexperienced. For example, Temple (1987) studied the predator-prey relationships between the red-tailed hawk (*Buteo jamaicensis*) and three of its prey. He found that substandard prey were not preferentially attacked, but were usually easier to capture and kill because they were unable to escape or defend themselves as well as normal individuals. The implication is that an inexperienced reintroduced animal is at higher risk of predation than an experienced wild animal.

1.4 How chances of survival after reintroduction can be maximised.

Reintroduction necessarily involves liberating animals into the wild environment. Various release techniques have been developed to maximise the chances of a successful reintroduction. One of the most primitive reintroduction techniques involves merely transporting the animals to the release site and letting them go ("hard-release"). Alternatively, "soft-release" involves temporarily housing previously captive-reared animals at the release site allowing acclimatization to the local wild habitat, before all captive-rearing protection is withdrawn (Kleiman 1989). It is difficult to use "soft-release" techniques when readying animals for predators because of the potentially terminal nature of the interaction involved. However, some programmes have achieved an effect similar to "soft release" for predators (Soderquist in press), and releasing animals in a predator trapped area approximates the "soft-release" criteria (Maloney pers. comm.).

A method that can be used in conjunction with, or instead of, "soft release" to prepare captive-reared animals for predators is to train them to be fearful of predators. Antipredator-training by conditioning should teach captive-reared animals to be more wary of predators. The notion of conditioning animals to respond to stimuli is a well-known concept. However, only recently has its potential been recognised in the conservation framework.

1.5 Teaching predator recognition.

Most animals have the ability to recognize predators and respond to them (Klump & Shalter 1984; Morse 1980; Seyfarth & Cheney 1990) and predator recognition often has a strong innate component (Magurran 1990; Owings & Coss 1977; Smith 1976). But responses of animals to predators are also strongly influenced by experience (Conover 1987; Hinde 1970; Veith et al. 1980). Experience is also important in recognition of enemies by birds, including nest parasites (e.g., cowbirds, Smith et al. 1984) and predators (Curio 1975; Smith 1986).

The ability to deal with enemies may be considered a two stage process (McLean and Rhodes 1991). First, the animals must learn to recognise the predator as a dangerous object. Discrimination between dangerous and harmless situations is necessary if prey animals are to actively avoid predation, and avoid wasting energy on unnecessary responses (Robinson 1980). In this thesis, this discriminative process will be referred to as predator recognition. Second, once the animals can recognise a predator as dangerous, they must learn ways of dealing with that predator. Improved recognition abilities should give otherwise naive animals a preliminary advantage when they first encounter a predator.

Conditioning involves the appropriate pairing of a neutral, or conditioned stimulus (CS) with a known noxious, or unconditioned stimulus (US) (Mazur 1990). Such pairing of stimuli results in the linking of a previously unrelated response or conditioned response (CR) to an initially neutral stimulus (US). In behavioural studies a change in CR motivational state cannot be observed directly, and is thus studied indirectly by observing a change in behaviour. Any behavioural change is interpreted as an index of the response, and where conditioning aims to teach an animal to recognise a predator as dangerous, this response is referred to as antipredator, or predator recognition behaviour. Predator recognition may be indicated in three ways. First, by the prey animal performing overtly defensive behaviours, such as fleeing or hiding; second, by attacking the predator (e.g., mobbing), or third, by performing behavioural patterns that differ from its normal behaviour (e.g., stotting in gazelles, Caro 1986; and alarm calling in ground squirrels, Sherman 1977).

Behavioural responses often contain elements of individual variability, and in order to cope with animals of the same species responding to the same stimulus in different ways, but with equivalent intensity, some researchers (Robertson & Norman

1976; Giles & Huntingford 1984; Maloney & McLean in press) have developed and used compound measures of responding. Compound measures are useful because they take into consideration the many behaviours that occur in response to a stimulus, and also can include adjustment for the intensity of each behaviour.

An example of the use of conditioning techniques to enhance predator avoidance was a study conducted with Siberian polecats by Miller et al. (1990). Polecats experienced a mild aversive stimuli (US = being shot by a rubber band) presented in tandem with predator models (CS) to enhance predator avoidance (CR). The polecat study shows that it is possible to simulate aversive events, and conduct successful conditioning experiments, without causing long-lasting injury. This is important especially when working with endangered species, where injury to individuals must be minimised. Examples of other studies which link conditioning to predator recognition are shown in Table I. Of the studies listed, only those conducted in the last five years utilize antipredator conditioning to training captive-reared individuals prior to release. The most recent studies consider the possibilities of antipredator-training for endangered species destined for reintroduction (Miller et al. 1990; Hölzer et al. in press; Maloney & McLean in press; McLean et al. in press).

The development of techniques to teach coping skills has only recently been attempted (Hölzer, work in progress) and is beyond the scope of this thesis. Although, where appropriate coping responses are known, it should be possible to train animals to exhibit antipredator behaviours to predators.

Table I. Previous studies of conditioned predator recognition.

STUDY ANIMAL	CONDITIONED STIMULUS	UNCONDITIONED STIMULUS	SOURCE (order by year)
White-throated sparrows	live: Blue jay Squirrel	adult sparrow distress calls	Stefanski & Falls (1972)
European blackbird	models: owl noisy friar bird non-natural object	adult blackbird "tutor"	Curio et al. (1978)
European blackbird	models: noisy friar bird non-natural object	adult blackbird mobbing calls multispecies mobbing calls live blackbird adult tutor	Veith et al. (1980)
Starlings	model owl	model clutching live starling adult starling alarm calls model clutching dead starling	Conover & Perito (1981)
American crow	model Great horned owl	model clutching dead crow	Conover (1985)
Siberian polecat[1]	models: owl badger	shot with rubber band	Miller et al. (1990)
	live dog	threatening dog interactions	
Atlantic salmon smolt[2]	live cod	contact and non-contact with cod	Järvi & Uglem (1993)
Fathead minnows	chemical: of pike predator	chemical: minnow alarm substance	Chivers & Smith (1994)
Rufous hare wallaby[1]	models: fox cat	wallaby alarms + noxious noise lunge by model + water squirts	McLean et al. (in press)
New Zealand robins	model stoat	adult robin alarm & distress calls	Maloney & McLean (in press)
Takahe[1]	model stoat	model "attacks" takahe chicks takahe hand-puppet "fights-back" predator model	Hölzer (work in progress)

[1] Work on endangered species in captive environments for reintroduction into the wild.
[2] Hatchery reared for reintroduction into wild habitat.

1.6 Antipredator-training of a species reared in captivity: necessity and techniques.

Black stilts (*H. novaezealandiae*) are endemic to New Zealand and their numbers have declined dramatically over the last 100 years (Pierce 1980). A major reason for this decline is believed to be the impact of mammalian predators introduced to New Zealand in the past 100-1000 years (Pierce 1984). It is not uncommon, following introductions of exotic species by humans, for predators to drive prey to extinction (Savidge 1987). Black stilts and mammalian predators do not share a common evolutionary history, thus black stilts do not have strong antipredator responses to mammalian predators, although they respond appropriately to aerial predators (Pierce 1986).

In an effort to conserve black stilts, the Department of Conservation (DoC, previously the Wildlife Service) initiated a management programme in the 1980's. A major objective was the establishment of a captive-rearing programme, involving raising young black stilts in a predator-fenced aviary complex and releasing them at approximately nine months of age. Wild-reared juvenile black stilts remain with their parents for approximately nine months and during this period of semi-dependence it is believed that juvenile birds learn a number of skills from their parents (Pierce 1980). The most important survival skills for black stilts include effective foraging techniques, roost site selection and predator recognition and response. Managers aim to have the rearing aviaries imitate natural habitat, although the effectiveness of such a rearing environment is currently unknown. Another MSc. project (L. Adams) is examining survival skills of captive-reared black stilts after they have been released.

The black stilt rearing aviaries also house a small number of pairs of adult birds, and the area around the aviaries provides feeding and nesting habitat for a number of river and wetland birds (e.g., pukeko *Porphyrio melanotus*, spur-winged plover *Vanellus miles novaehollandiae*, South Island pied oystercatcher *Haematopus finschi*, pied stilt *Himantopus leucocephalus*, banded dotterel *Charadrius bicinctus*, and duck species). Harriers (*Circus approximans*) frequently fly over the captive-rearing complex (pers. obs.). Therefore, captive-reared black stilt juveniles can potentially learn about this aerial predator by exposure to conspecific and multispecific alarm calling in response to an aerial threat. Because juvenile black stilts are hand-raised in an area free of ground-predators, some researchers (e.g., Pierce 1982; Maloney pers.

comm.) have speculated that these birds are naive to mammalian predators. Pierce (1982) recommended that no further liberations of captive-reared black stilts be attempted until the habitat in the captive-rearing enclosures more closely resembled the wild environment, and precautions had been taken to ensure that the birds destined for release were wary of predators.

Rachlin (1976) proposed the idea of preparedness, suggesting that animals need not be born with a fear of cats, but rather are born with a disposition to acquire such a fear through classical conditioning. Because black stilts have historically lived in a situation free of mammalian predators in New Zealand, they are not considered to be "prepared" for recognition of mammalian predators. However, black stilts may have *the propensity to learn* to recognise mammalian predators, and therefore benefit from antipredator-training. Black stilts may have been exposed to avian ground predators in the evolutionary past (e.g., weka, *Gallirallus australis*), hence may have a disposition to learn about ground predators.

Antipredator-training does not aim to increase the general mammalian predator response in black stilts. Behaviours are not infinitely malleable, therefore learning can only produce changes in behaviour within the constraints of the animals' innate ability (Domjan & Burkhard, 1982). However, conditioning should enable the trained birds to recognize a mammalian predator as dangerous. They can subsequently use existing antipredator responses from their behavioural repertoire to escape capture. Improved recognition can potentially provide a "crutch" for the birds' survival during the critical post-release period when they are most at risk in a new environment.

1.7 Aims

In this thesis I investigated the possibility of using antipredator-training to teach hand-reared black stilts to be wary of cats. There were two main aims:

(a) to test whether captive-reared black stilts could be taught to recognize a mammalian predator that they were likely to encounter once released into the wild (examined by two experiments in Chapter 2).

(b) to suggest how antipredator-training could be integrated into the black stilt management strategy; and possibly used in other situations where animals are captive-reared for reintroduction into the wild (Chapter 3).

1.7.1 Questions

I addressed four questions (terms explained in Table II):

(1) **What are the responses of captive-reared black stilts towards the cat model prior to training (i.e. baseline recognition)?**

Background: None of the birds have experienced the models before, either in their life time, or historically.

Prediction 1: *Response to cat model = response to novel control object.*

(2) **Does antipredator-training increase recognition of cats as predators by black stilts?**

Background: Antipredator-training through conditioning has been effective in other studies.

Prediction 2: (a) *Responses to cat model: Post-Training Test > Pre-Training Test.*

(b) *Post-Training responses: cat model > control object.*

(3) **Do antipredator-trained black stilts respond differently to the cat model than individuals that received no training?**

Background: Previous studies have shown that trained individuals exhibit responses superior to untrained animals, in reaction to the training model.

Prediction 3: *Responses to cat model: trained stilts > untrained stilts.*

(4) **Do responses exhibited by black stilts in (2) and (3) change over time?**

Background: Processes such as maturation, forgetting, habituation and response extinction are likely to change the animals' responses over time.

Prediction 4: *Response* $T_o \neq$ *response* T_n; where T_o = a previous Test, and T_n = a Test at a later time.

Experiment I involved antipredator-training of approximately two thirds of the 1992/93 captive-reared juvenile black stilts, with the remaining birds Tested but Untrained. Therefore, Experiment I primarily examined questions (2) and (3). All of the 1993/94 captive-reared black stilt juveniles received Training in Experiment II. Training and Testing of responses occurred at different ages and involved cat and control models. Therefore, Experiment II addressed questions (1), (2) and (4).

1.8 Study animal

The black stilt is a critically endangered wading bird, which breeds only in rivers and wetlands in the Mackenzie Basin region (central South Island of New Zealand). There are currently 72 wild black stilts, and less than 20 breeding pairs. All birds are intensively managed by DoC.

The ancestors of the black stilt are thought to have originated from Australia (Pierce, 1980), and the black stilt was widespread throughout New Zealand prior to human colonization. With humans came the introduction of mammalian predators such as the cat and various species of mustelids (*Mustela spp*) and rats (*Rattus spp*). As many aspects of black stilt morphology and ecology developed in the absence of mammalian predators, black stilts were apparently ill-equipped to cope effectively with the onslaught of a new and efficient type of predator (Pierce 1986). Pierce (1980) considered the main reason for the massive decrease in black stilt numbers and distribution to be predation; mainly by feral cats (which are known to prey on eggs, chicks and adults; Pierce 1982), mustelids and norway and ship rats, all of which were widespread in New Zealand river valleys by the late nineteenth century (Bull 1969 cited in Pierce 1980, Pierce 1982).

After the introduction of mammalian predators and European land management techniques, black stilt distribution progressively decreased (Pierce 1982). Secondary reasons for the diminishing black stilt population included human destruction of physical habitat and hybridization with a close relative of the black stilt, the pied stilt (Pierce 1982). Available habitat was reduced by flooding, drainage or controlled flow regimes of rivers due to hydro-electricity works, weed invasion and river protection work. For example, a clear effect of drainage was the loss of habitat area. However, the negative effects of weed invasion include both quantitative and qualitative loss of

habitat, as the presence of vegetation in riverbed areas provides cover, allowing predators to approach birds. Hybridization with pied stilts occurs, despite positive assortive mating of black stilts (Pierce 1984) due to the relatively low availability of black stilts as mates.

During the 1970's, in an effort to conserve the remaining black stilt population, the New Zealand Wildlife Service and later DoC began an active management programme. In 1987 DoC built a captive breeding centre three km south of Twizel. The first captive hand-reared juveniles (3) were released from Twizel in 1987, and the numbers of birds raised and released has recently been increased due to increased size of holding facilities and changes in management practices. The first of these large releases was of 34 captive-reared birds in September 1993.

Chapter 2

METHODS and RESULTS

2.1 General methods.

2.1.1 Definition of Terms.

Two experiments were performed which addressed different, but overlapping questions. The general research design was similar for both experiments, but some differences in detail occurred in Experiment II as a consequence of the experience gained during running of Experiment I.

The general design involved comparing behaviours of juvenile black stilts, exhibited in response to a model cat during Tests conducted before (*Pre-Test*) and after (*Post-Test*) antipredator-*training*. Table II explains each of these italicised terms, and differences in design between Experiments I and II. All methodological details and terms apply to both experiments unless otherwise stated.

All Test sessions and the morning Training sessions were conducted 1-3 hours after sunrise. All Training and Testing occurred in the enclosures where the birds were normally housed.

Experiment I (1992/93 field season) compared behavioural responses of juveniles that received antipredator-training, with those that did not. For Experiment I all birds were randomly assigned to one of two conditions, Trained or Untrained.

Experiment II (1993/94 field season) involved the antipredator-training of all birds, followed by testing of their responses to the predator and control models. In addition to the within-age comparisons, I also tested responses of birds at different times (i.e. between-age). The time between Tests at each age acts as a measure of the habituation to the stimulus and retention of learning from the previous Training day. Due to small subject numbers in between-age comparisons in Experiment I, only data from Training and Testing in Experiment II were used to examine a possible age-related learning effect.

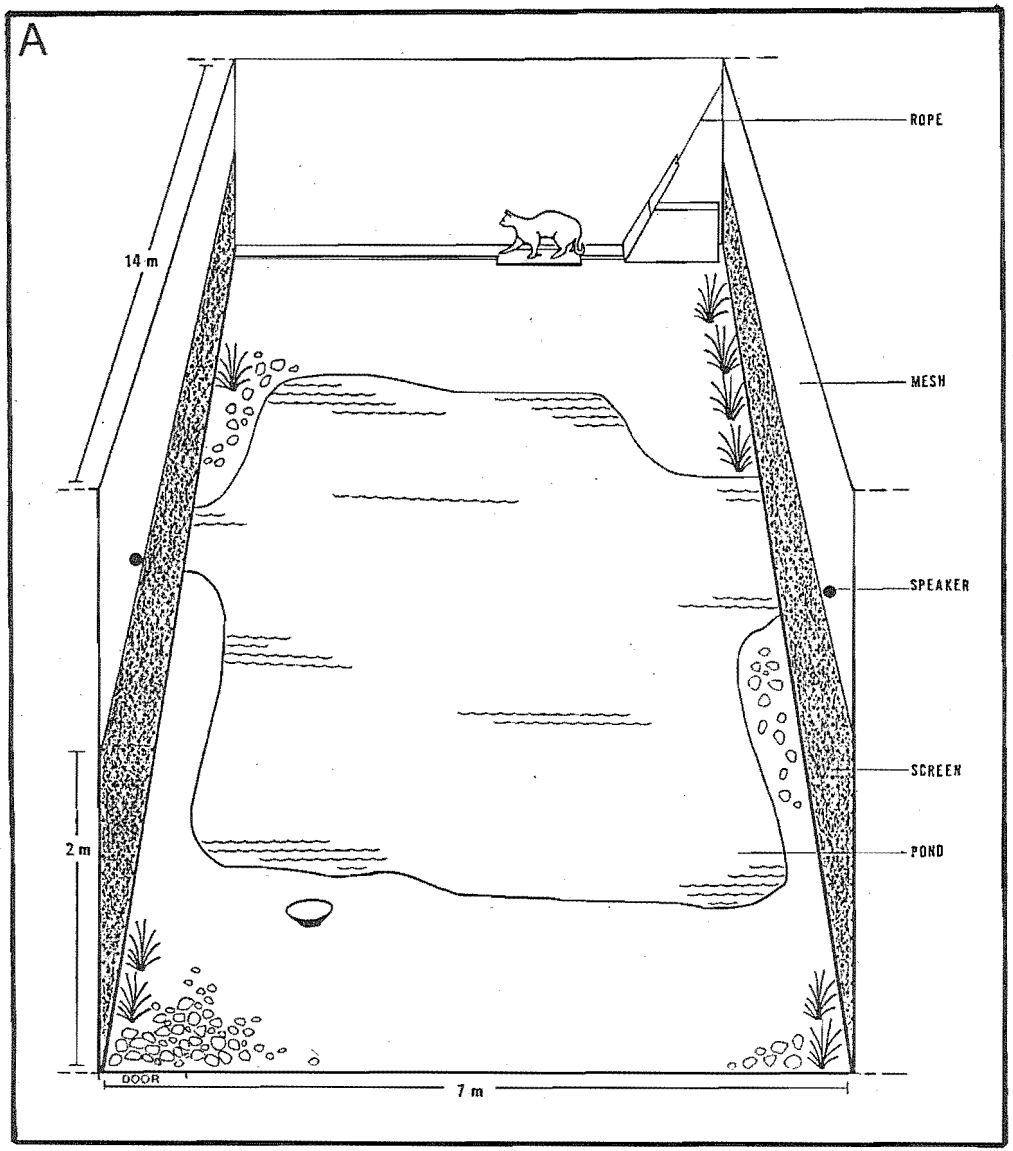
Table II. Explanation of terms (highlighted) and Test/Training conditions for Experiments I and II.

DAY	TREATMENT AND DESCRIPTION	EXPERIMENT	
		I	II
1	**Pre-Test**: presentation of *Test* model for a fixed period.		
	Test Model(s)[1]	mounted cat	mounted cat papier-mâché object
	Duration	220s	180s
2	**Training**: a number of training *sessions* during the day. Each training session consists of a number of training *episodes*, made up of the presentation of the *training stimulus*, separated by fixed periods of silence. The training stimulus is the pairing of the presentation of the training model (mounted cat) and alarm call playbacks.		
	# sessions @ duration	3 @ 220s	2 @ 120s
	# episodes @ duration	4 @ 40s	2 @ 30s
	Model appears + playback	concurrently	model 2-5s prior
	Inter-episode silence	20s	30s
3	**Post-Test**: presentation of Test model for fixed period.		
	Test Model(s)	mounted cat	mounted cat papier-mâché object
	Duration	220s	180s
4	**Post-Test**: presentation of the Test model not presented on Day 3, for fixed period.		
	Test Model(s)	n/a	mounted cat papier-mâché object
	Duration	n/a	180s

[1] Models pictured in Fig. 2.

2.1.2 Study animal and Sites

This study was conducted with 63 captive-reared black stilts over two rearing seasons (November 1992-September 1994). All work took place at the Department of Conservation black stilt captive-rearing complex in Twizel, New Zealand.



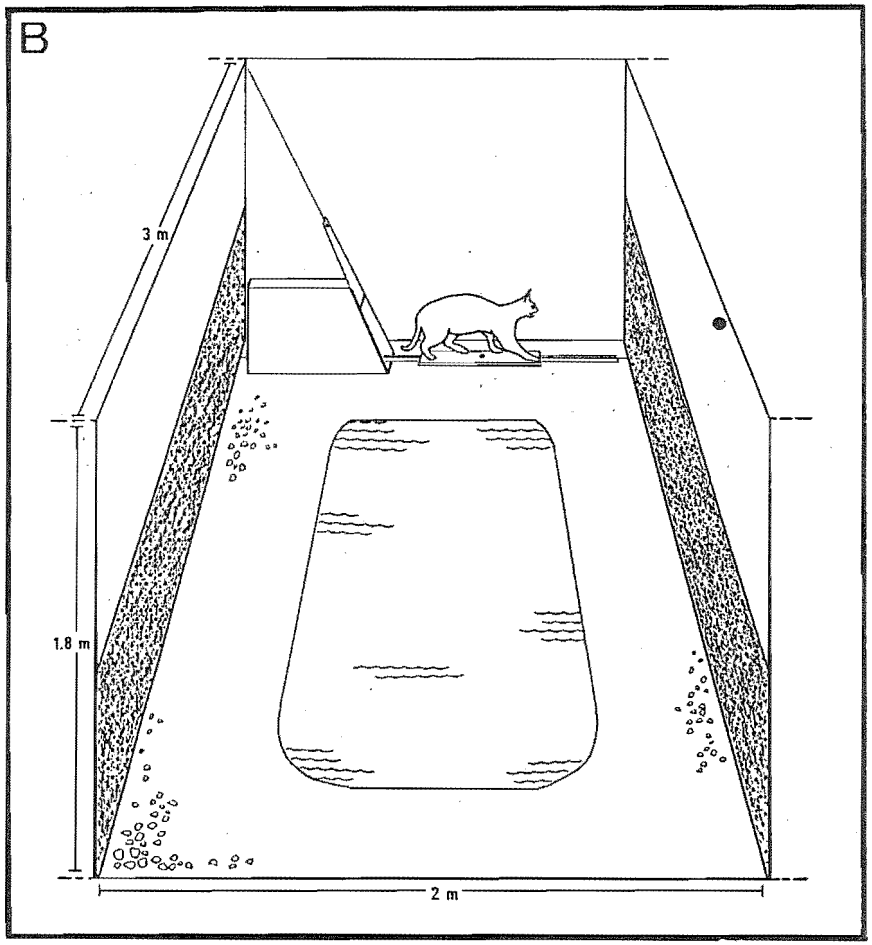


Figure 1: Design of aviary enclosures, with experimental apparatus for antipredator-training experiments in place. Models are mounted on trolleys, which are able to move along the rail during Testing and Training. The cat model is pictured in position for Testing. A) large enclosure (all labels apply to B also); B) brooder enclosure. Exact details of methodology and apparatus given in text.

From hatching until 1 month of age the birds were unable to fly and were housed in small brooder aviaries (3m x 2m x 2m). The brooder enclosures consisted of approximately two thirds river shingle and one third water pond (Fig. 1b). Once the juveniles were flying (at 30-40 days) they are moved into a larger enclosure in one of three aviaries. Each large aviary consisted of 4 or 7 enclosures (14m x 7m x 6m), all with similar proportions and arrangements of tussock vegetation, river shingle and flowing water (Fig. 1a).

Visual, auditory and olfactory communication was possible between enclosures of all aviaries. During Training and Testing each aviary enclosure was visually isolated from adjacent enclosures by double thickness hessian screens. All individuals were housed in clutch-sized groups of 3-4 birds (usually siblings). Clutch composition was dependent on time of hatching, so some clutches consisted of siblings, while some were of mixed parentage. Birds were individually marked by combinations of two colour bands on each tarsus. Birds were fed twice daily (at approximately 0830 and 1500 hrs), generally by a person entering the enclosure, and were therefore accustomed to human presence. Where possible, experimental treatments occurred after feeding.

2.1.3 Stimuli and apparatus

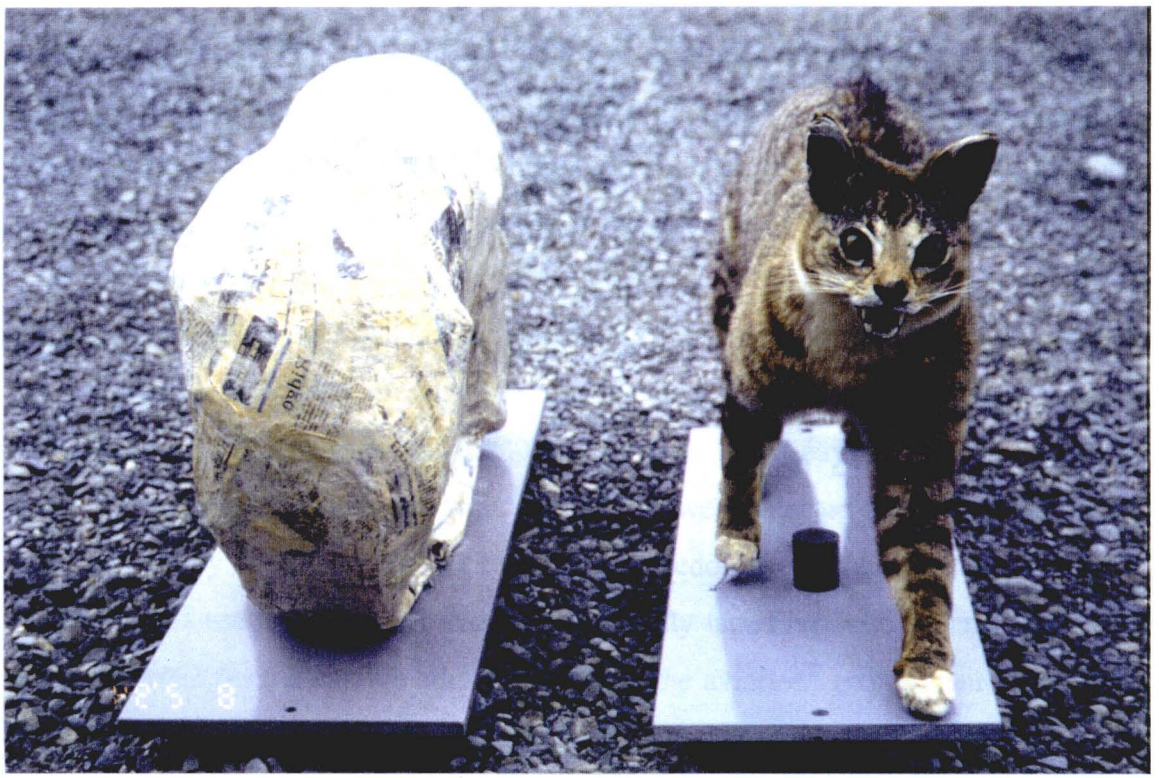
2.1.3.1 Conditioned and Test Stimuli.

In both experiments, the predator model used during Tests and Training was a mounted feral cat in a walking stalk-like posture. The control model presented during Experiment II Tests was a papier-mâché object of approximately the same dimensions as the cat model (Fig. 2).

A grey plastic box (0.9m x 0.7m x 0.4m) with a front opening hatch was placed inside the aviary enclosure, and hid the models from the birds. The box was always placed on the side of the aviary away from the observer (see Fig. 1). Box position was constant for within-age Tests, but varied between Tests at different ages (e.g., box in far left corner for age 1 treatment, and at far right for age 2).

Models were mounted on small trolleys that moved easily on a 0.05m wide rail which ran from the box across the width of the aviary. A simple system of ropes, was used to open and close the box hatch and move the models along the track. Additional ropes enabled each model to be turned up to 90° towards the birds and back to its original position while moving forward or backward on the rail.

a)



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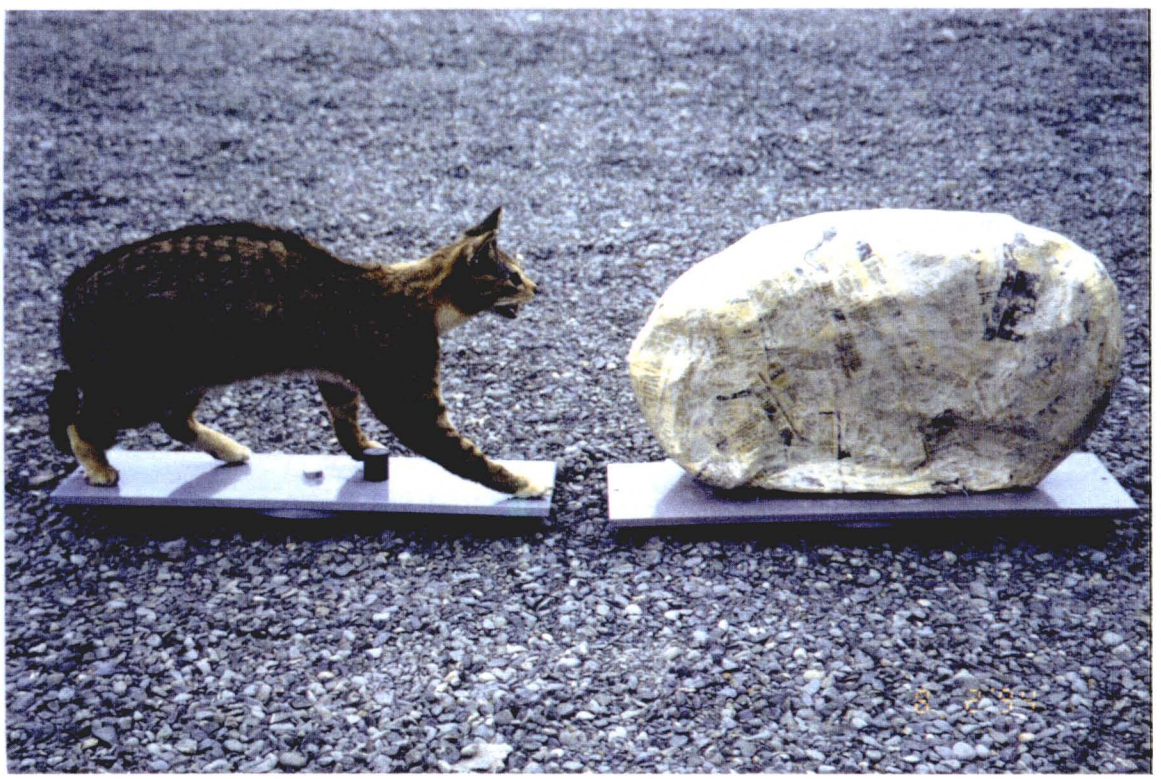

Figure 2: The two models used in this study were a mounted feral cat and a papier mâché control object. a) front view of models, b) side view.

2.1.3.2 Recording of Observations.

All experimental observations were recorded with a tripod-mounted VHS Movie camera (Panasonic NV-M40A) fitted with a wide angle zoom lens. Video recording began after 10 min into a 15 min settling period, and continued for 5 mins after the Test or Training had finished. A 2 m high hessian screen positioned 8.5 m in front of the aviary shielded the camera, observer(s) and equipment from the stilts.

2.1.3.3 Unconditioned Stimuli and Playback Recordings.

The auditory stimuli presented during Training were avian alarm calls. Alarm calls were recorded using a Sony TC-D5M recorder and a bayerdynamic TG X480 microphone in a hand-held parabolic dish. Calls were selected for use on the basis of species, variety of calls, recording quality and freedom from background noise. Experiment I used repeat playbacks of sequentially taped black stilt alarm and distress calls recorded from a captive adult pair held in the aviaries. Experiment II used black stilt, pied stilt, South Island pied oystercatcher and spur-winged plover alarm calls recorded at the species' nesting sites in response to human presence. Calls were dubbed concurrently onto a single tape to produce a continuous call sequence including all species. To avoid habituation to the playback, each Training session used different playbacks of multispecific alarms. The same playback was used for Training sessions of the same age groups (e.g., all the birds received the same playback when Trained at 1 mth, and all received an alternative playback at 6 mths). All calls were played using a cassette tape recorder (Sanyo M1001A) and battery powered Realistic speakers (0.14 m x 0.08 m x 0.08 m). The volume of the alarm calls heard in the aviary was matched by ear to approximate the volume of natural alarm responses given by those species in the playback, at an equivalent distance. During non-training days, real speakers were replaced with similar looking dummies. In the brooder aviary, speakers were located near the roof of the aviary, and away from the cat model (Fig. 1b). In the large aviary, speakers were mounted on the sides of the aviary, approximately 10 m away from the box or model and 2 m above the ground (Fig. 1a).

2.1.3.4 Brooder aviary.

Experimental apparatus was positioned during routine daily cleaning of the aviaries. All experimental apparatus wash positioned (Fig. 1b) inside the aviaries for

at least a day before the manipulations began. Each Test/Training began by the observer using ropes to lift the box hatch and cause the model to emerge onto a 1 m long rail. After the Test or Training the model was pulled back into the box and the hatch shut. The observer left the hide unnoticed 5 mins after the end of the Testing or Training session.

2.1.3.5 Large aviary.

When working with birds in the larger aviaries it was not possible to prevent the birds from being present while the apparatus was set up. Intrusions into the aviary were minimal and did not exceed the disturbance caused by normal aviary maintenance (e.g., weeding of enclosures). Care was always taken that the models were hidden from the birds while being put in position. The aviary was approached in a small white car, which was parked behind the screen where the observers set up the video camera. Trucks and motorbikes were commonly used inside and around the aviary complex and the birds were accustomed to vehicles. Because of the size of the aviary (7 m x 14 m x 6 m), two observers were required to erect the apparatus and to conduct the experiment. One person kept the video camera directed at the birds, while the other operated the rope system, located individual birds inside the aviary and recorded their relative positions into the microphone on the video camera throughout the treatment. Settling periods, videoing and end of Testing and Training details were as described for the brooder aviary (section 2.1.3.4).

2.1.4 Behavioural Data Recorded

All behavioural and sampling details were determined prior to the experiments by *ad libitum* sampling of juvenile black stilts in captivity. Each bird's response to the model was recorded using 19 non-mutually exclusive behavioural categories and three different sampling techniques (Table III).

Distance estimates were based on the position of each bird relative to pre-established reference points within the aviary. Behaviours were transcribed from video tape in 10s periods for the duration of the Test and standardized for Tests of differing lengths. Where environmental "noise" (e.g., plane overhead) obviously affected the birds' responses, the behavioural response figures were calculated using the data collected prior to the interruption.

Table III. Behavioural ethogram for the juvenile black stilts and a description of behaviours, distances, definitions and recording methods.

RESPONSE	RECORDED AS (per 10s)	DESCRIPTION
Stepping	All occurrence/bird	Foot raised and lowered
Head bobbing	All occurrence/bird	Rapid vertical movement of neck
Flight	All occurrence/bird	Wings flapping, bird left ground > 1 wing flap
Hop and flap	All occurrence/bird	Wings flapping, bird left ground < 1 wing flap
Calling	All occurrence/clutch	Alarm and other vocalization
Run and freeze	Presence/absence	Run and drop to the ground, only at pre-fledging
Hunch	Presence/absence	Hunched posture, while stationary or moving
Upright posture	Presence/absence	Stand erect, neck extended upwards
Forward posture	Presence/absence	Stand erect, neck extended forwards
Walk fence	Presence/absence	Head/body orientated at fence, and bird moving
Comfort movements	Presence/absence	Various. Categorized as e.g., stretch, shake
Preening	Presence/absence	Grooming using bill, head or feet
Foraging	Presence/absence	Bill used to peck or swipe substrate or food
Resting	Presence/absence	Sitting, or standing on one leg
Head tilt	Presence/absence	Head tilted at 30-90° skyward
Head orientation	Instantaneous	Head facing towards/away/side-on to model
Model distance (m)	Instantaneous	Bird's physical position, relative to model
Substrate	Instantaneous	Substrate bird standing on - shingle, water
Cover	Instantaneous	Is the bird in line of sight of the cat (Yes/No)

2.1.4.1 Composite Agitation Score (CAS). I combined a set of behaviours and proximity measures into an index to create an overall agitation response score for each Test (c.f. Giles & Huntingford 1984; Maloney & McLean in press). The behavioural categories and their respective contribution to the CAS, are presented in Table IV. Only activities that appeared to indicate recognition were included in the scale (see Appendix I for justification of individual behaviour score assignment). For example, the behaviour "head tilt" (Table III) appeared to be more dependent on air traffic and birds flying overhead than on anything occurring within the aviary enclosure, and was therefore not used in the CAS. Each behaviour was divided into three categories and assigned values of 0 (no or low response) to 2 (strong response). By adding the score for each behaviour, a CAS was attained (maximum possible score of 21). The CAS is assumed to be positively correlated with predator recognition (refer Appendix I). The CAS was only calculated from data gathered in the large aviaries in the 1993/94 season.

Table IV. Composite Agitation Score (CAS) for black stilt behaviours and for a distance measure.

BEHAVIOUR & DISTANCE MEASURE OF STILT[1]	INTENSITY SCORE[2] 0	1	2
Number/10 sec observation periods:			
Steps	5-10	<5	>10
Head bobs	0<0.5	0.5-1.5	>1.5
Presence during Test (max. 100%):			
Upright postures	0%	<30%	>30%
Forward postures	0%	<20%	>20%
Foraging	present	-	absent
Preening	present	absent	-
Total number[3] of:			
Hop and Flaps	0	1	≥2
Flights	0	1	≥2
Alarm Calls[4]	0	1-10	>10
Resting	present	-	absent
Distance from model averaged over Test (max = 14m):	<3m	3-7m	>7m

[1] Descriptions of behaviours and distance measure as per Table III.
[2] Criteria for ascribing scores as per Appendix I.
[3] Number adjusted for different times in Recognition Tests (2 min) and the 6 and 9 month Tests (3 min).
[4] The same total value is given to every member of the same clutch.

2.1.4.2 Training Response Intensity Scale (TRIS). The magnitude of antipredator response in Post-Training Tests could depend on the quality of the response during Training. I therefore developed a second subjective response scale for the Training data. The four point (0-3) scale for the video record of Training (Table V) attempted to quantify the overall alarm intensity of the birds during Training. Training consisted of two episodes per session, and two sessions per day (Table II). Each Training episode was rated from 0 (no response) to 3 (strong response). For each clutch the final TRIS consisted of the sum of the four Training episode scores for the day. The behavioural responses used as indicators of Training intensity differed between the brooder and large aviaries, but the 0-3 scoring of response remained consistent (Table V). The TRIS was only calculated from the 1993/94 Training data, and allowed comparisons of Training responses to be made between brooder and large aviaries.

Table V. Training Response Intensity Scale (TRIS) and criteria, as applied to Training episodes for black stilt clutches used in Experiment II.

AVIARY	INTENSITY SCORE			
	0	1	2	3
Brooder	No response	Generally alert & agitated behaviour	<33% freeze & escape behaviour	>33% freeze & escape behaviour
Large	No response	Alert, stay in similar position	<33% flying, calling & moving away	>33% flying, calling & moving away

2.1.5 Analyses of Data

In both experiments, each bird acted as its own control (i.e. a paired design) with the major comparisons being made between matched responses before and after Training. Thus all analyses were conducted using complete data sets (i.e. no birds received incomplete treatments, and for comparisons in the same aviary-type, data was omitted for birds that died before the end of the experiment).

All Training and Testing was conducted while the birds were in clutch groups. Because birds could see their clutch mates, responding of each individual to the stimuli was not independent. One way of coping with the lack of independence would be to only use the responses of one bird per clutch, or to average the response of the clutch. However, the number of clutches was so small (10 and 9 in Experiments I and II respectively) that using one data point per clutch reduces the available degrees of freedom for each statistical test to less than 10. Data from every individual was used in statistical analyses, not just one bird per clutch. The data collected in these experiments were not normally distributed and were not responsive to transformation, thus multi-factor ANOVA designs were not appropriate. Conservative statistical testing was achieved by conducting two-tailed non-parametric tests with an acceptance level for statistical significance set at $p<0.01$ (Maloney & McLean in press for background on setting significance acceptance values), although cases of marginal significance are also reported.

Effects of Training were tested in Experiment I by examining the behavioural responses before (Pre-Tests) and after (Post-Tests) Training for both Trained and Untrained individuals, using Wilcoxon Sign Rank tests for paired samples. The main effect of Training is looked for by comparing the *relative* difference in responding in Trained and Untrained birds (i.e. Post-Test responses minus Pre-Test responses of Trained birds c.f. the same response difference in Untrained birds) using Mann-Whitney U tests for two-sample data.

The analyses of Tests conducted in the brooder aviaries in Experiment II investigated whether the initial response given to a model was a function of the type of model. This *Pre-Test model effect* was examined using Mann-Whitney U tests and by comparing the Pre-Test responses of the birds that saw the cat model with the Pre-Test responses of the birds that saw the control model. Differences in behavioural responses due to Training (i.e. responses to a model in Pre-Test compared to responses to the same model in the Post-Test, referred to as a *Training effect*) were examined using Wilcoxon Sign Rank tests for paired samples. Differential recognition of the models after Training (i.e. a *Post-Test model effect*) was investigated by comparing Post-Test responses to the cat model, to Post-Test responses to the control model, using Wilcoxon Sign Rank tests for paired samples.

Analyses of results from the birds in large aviaries in Experiment II tested for a *Training effect* (i.e. difference in Pre-Test and Post-Tests response to the cat model), a *model effect* (i.e. a difference in Post-Test responses to the cat and control models), an effect of intensity of responding during Training, and changes in response over time. The Training and model effects were examined by using Wilcoxon Sign Rank tests for paired samples, as for the Training effect in the brooder aviary. The relationship between response during Pre- and Post-Tests, and response during Training, was investigated by comparing Composite Agitation Scores (CAS, refer Table IV) at 6 and 8 mths with Training Response Intensity Scores using Spearman's rank correlations. Changes in behavioural response over time, indicating retention and efficacy of learning, were examined using Wilcoxon Sign Rank tests for paired data. CAS of Post-Test responses of stilts towards the cat model, from the 2 mth Recognition Test, were compared to Pre-Test Scores for birds at 6 mths. A similar comparison was made using Post-Test CAS at 6 mths and Pre-Test Scores at 8 mths. The efficacy of learning due to Training at 6 and 8 mths was investigated using Wilcoxon Sign Rank tests for paired data, where the difference in CAS (i.e. Post-Training Test minus Pre-

Training Test) were compared. The Post-Training Test response to each model was compared at age 6 and 8 mths using Wilcoxon Sign Rank tests for paired data.

In both Experiments I and II, Kruskal-Wallis tests were used to identify any possible confounding effects of clutch (i.e. less variation within than between clutches), parentage, number of individuals in clutch, sex, or order of model presentation. Details of which birds were dead (or missing and presumed dead after 3 mths, Adams 1995) were tested against pre-release CAS using Kruskal-Wallis tests. Data are not always presented for all tests; they are given when significant (including marginal significance) effects were found.

2.2 EXPERIMENT I: The effect of antipredator-training on cat model recognition.

The first experiment was conducted between November 1992 and September 1993, to determine whether Training of juvenile black stilts which are reared in captivity could increase recognition of a cat model. Comparisons were made between Pre- and Post-Test responses for each individual, and between Trained and Untrained birds. The cat model was presented to all birds (n=33, 10 clutches) on Test Days (Days 2 & 3) of the experiment. Six clutches (21 birds) received Training episodes on Day 2, and four clutches (12 birds) remained Untrained, and received no manipulation on Day 2.

2.2.1 Procedure

Clutches were randomly assigned to the Trained or Untrained condition. All birds received the experimental regime at age 40-50 d while still in the brooder aviary (Table VI). Depending on age and experimental condition, some clutches also received treatment at an additional age (Table VI).

Each Training and Testing treatment was conducted over three days as follows:

Day 1 **Pre-Test** (measuring baseline response to cat model)

The cat model was pulled approximately 1 m out of the box. The model remained stationary for 220s, and was then retracted backwards into the box.

Day 2 **Training Day** (behavioural conditioning episodes; no manipulation for Untrained individuals)

The cat model was pulled into the cage at the onset of playback of 40s of black stilt alarm and distress calls. While the calls were playing the cat model was moved along the rail away from the box. Retraction of the cat model into the box corresponded to the cessation of the alarm playback. The cat model was then hidden in the box for a 20s period. The Training episode was repeated four times, then the box hatch was lowered and the cat hidden. The Training session was repeated at approximately 4 hour intervals for a total of three sessions of Training.

Day 3 **Post-Test** (e.g., measuring the Post-Training response to the cat model)

The Post-Test was performed at the same time of day and in the same way as the Pre-Test.

Table VI. Experiment I Training/no Training regime showing the number of individuals and clutches, the Training condition and the ages at which Training/no Training occurred.

CLUTCH (number of individuals)	CONDITION	AGE AT TRAINING/NO TRAINING (mths)[1]			
		1.5[2]	3.5	7	9
1 (3-4[3])	Untrained	+	+		
2 (3-4[3])	Trained	+	+		
3 (3)	Trained	+	+		
4 (3)	Trained	+		+	
5 (4)	Untrained	+		+	
6 (4)	Trained	+			
7 (3)	Trained	+			+
8 (2)	Untrained	+			+
9 (4)	Trained	+			
10 (3)	Untrained	+			

[1] For ease of presentation all ages are rounded to the nearest half month.
[2] Conducted in brooder aviaries, all other tests/training occurred in the large aviaries.
[3] 1 individual died after first treatment (death not related to this study).

2.2.2 Experiment I: Results

2.2.2.1 Overview of juvenile black stilts' responses to Testing and Training.

When the cat model was pulled into the brooder aviary for the first Pre-Test the juvenile black stilts responded with general alarm, followed by varying degrees of curiosity. The Training episodes were clearly frightening, and although behaviours were not specifically recorded, response during Training ranged from a high frequency of escape behaviours (e.g., "walk fence") to alarm calling and attempts to fly around the small enclosure, including hitting the aviary walls. Although not directly measured, the response intensity appeared to decrease throughout the Training day.

2.2.2.2 Effect of antipredator-training.

Relative to Pre-Test response levels, Trained birds showed decreased frequency of head bobbing (Wilcoxon, p=0.0002; Table VII) and upright postures (Wilcoxon, p=0.0004; Table VII) in Post-Tests. No TRAINING EFFECT (i.e. no significant difference between Pre- and Post-Test levels of responding) was found for foraging, flights, mean distance to model, alarm calling, or stepping (Table VII). Relative to Pre-Tests, Untrained birds foraged more (Wilcoxon, p=0.0143), maintained less distance from the cat model (Wilcoxon, p=0.0108) and decreased the frequency of upright postures (Wilcoxon, p=0.0024) in Post-Tests. No other behaviours significantly differed between Pre- and Post-Tests for Untrained birds.

However, only the relative increase in distance from the cat model differed significantly between Trained and Untrained birds (Mann-Whitney U, p=0.0013; Fig. 3); i.e. Post-Test minus Pre-Test responses of Trained birds was greater than the Post-Test minus Pre-Test responses of Untrained birds.

2.2.2.3 Data was affected by fixed methodological constraints.

The majority of behavioural data collected during Tests (Appendix II) showed consistent effects of parentage, number of individuals in a clutch, and factors related to birds being Tested in clutches (i.e. there was high between-clutch and low within-clutch variation; Kruskal-Wallis tests on individual behaviours, $p<0.05$). Responses were not significantly different between males and females. None of these results exceeded the significance p-value of 0.01; however consistent significance levels of $p<0.05$ indicated a trend.

Table VII. Experiment I: Effect of antipredator-training on behaviour of captive-reared black stilt juveniles in brooder enclosures.

BEHAVIOUR[1]	EFFECT	PRE-TEST[2]	POST-TEST	P
Distance**	Trained	2.08±0.05	2.15±0.08	ns
	Untrained	2.33±0.05	2.05±0.06	0.011
Foraging	Trained	0.07±0.03	0.14±0.04	ns
	Untrained	0.00±0.00	0.03±0.00	0.014
Flights	Trained	0.02±0.01	0.01±0.00	ns
	Untrained	0.01±0.01	0.00±0.01	ns
Head bobbing	Trained	1.34±0.26	0.20±0.05	0.001
	Untrained	1.56±0.33	1.31±0.24	ns
Stepping	Trained	6.40±0.57	7.02±0.57	ns
	Untrained	5.78±1.51	4.57±0.82	ns
Upright posture	Trained	0.46±0.05	0.20±0.03	0.001
	Untrained	0.42±0.06	0.17±0.03	0.002
Walk fence	Trained	0.18±0.04	0.33±0.07	ns
	Untrained	0.26±0.08	0.16±0.04	ns

[1] All behaviours are defined as per Table III. Figures shown are mean±standard error.
[2] The effect of Training immediately post-fledge is examined by comparing Pre-Test and Post-Test response levels for Trained (n=21) and Untrained (n=12) birds using Wilcoxon rank sum tests.
** indicates the only behavioural category where the difference in responses of Trained and Untrained birds were significantly different Mann-Whitney U, p<0.0013.

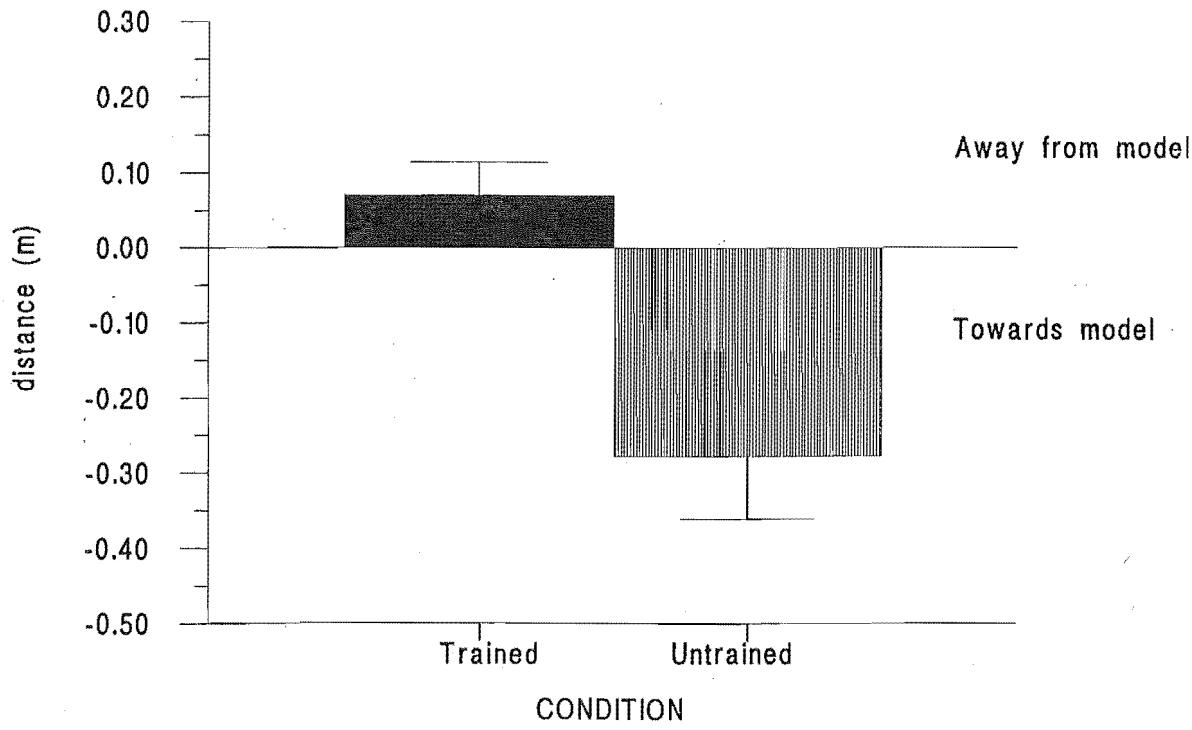

Figure 3: Experiment I: The relative change (Post-Test minus Pre-Test) in the distance maintained from the cat model was significantly greater for Trained (n=21) than Untrained (n=12) black stilts (Mann-Whitney U, p=0.0013). Standard error bars are shown.

2.2.2.4 Results from Training and Testing when the birds are older.

Small subject numbers, high individual variation and the strength of the clutch effect made it inappropriate to quantitatively test for effects of Training of black stilts at different ages (although this is examined in Experiment II). Generally, when the birds were older their responses were not as vigorous during Testing and Training compared to when they were Tested in the brooder enclosures at a younger age. Although not directly measured, behavioural responses elicited by Training seemed to decrease in intensity throughout the day of Training.

2.2.2.5 No effect of antipredator-training on post-release mortality.

With respect to the Training experiment, the birds that died after release (i.e. within 3 mths, including those birds classified as missing) were a random sample. The results indicate that there was no effect of Training on post-release mortality of captive-reared black stilts. However, low sample sizes mean that drawing conclusions about the success of antipredator-training based on post-release survival is inappropriate.

2.2.2.6 Results summary of Experiment I: The results of Experiment I showed that antipredator-training of young (40-50 d) black stilts increased the distance birds maintained from the predator model, suggesting that Trained juveniles recognised the cat model as more dangerous than their Untrained peers. Data were influenced by the rearing conditions for black stilts (i.e. birds were Tested with members of their clutch) and by parentage. Antipredator-training did not seem to affect post-release mortality of black stilts.

2.3 EXPERIMENT II: The effect of antipredator-training in model recognition and differentiation

Experiment II was conducted between November 1993 and August 1994. The primary differences between Experiments I and II were that in Experiment II all juveniles received antipredator-training and their ability to distinguish between a predator and control model was tested. Experiment II had two main aims: i) to test whether antipredator-training increased recognition of the cat model, and ii) to

determine whether any such recognition was discriminatory between the cat model and a control object in Post-Training Tests. Secondary aims for Experiment II were to investigate the initial responses of naive birds to novel objects, and whether learned responses changed over time. All birds (n=29, 9 clutches) received presentations of either the cat model or the control object on Test Days of the experiment (Table VIII). All birds were antipredator trained at three different ages. In addition to Testing at these ages, all birds also received a Recognition Test at approximately 2 mths old, one month after the first Training episodes.

2.3.1 Procedure.

Each Training and Testing treatment was conducted over four days as follows:

Day 1 **Pre-Training Test** (measuring baseline response levels. The first Pre-Test measured response to novel objects: a control object n=12, and a cat model, n=17)

The model was pulled approximately 1 m from the box, remained stationary for 180s, and was then retracted backwards into the box.

Day 2 **Training** (behavioural conditioning episodes)

The cat model was pulled into the cage 2-3s before 30s playback of multispecies alarm calls began. While the alarm calls were playing from the speaker the cat model was moved in a standard manner. In the small brooder aviaries the technique of movement was the same as for Experiment I (p. 25). In the large aviaries the cat model was pulled along a 6m rail (across the width of the aviary, Fig. 1a) for approximately 15s. After this time the model had reached the end of the rail and was rotated 90° towards the birds, then rotated back and withdrew backwards into the box for the remaining 15s of alarm calls. After a 30s pause in the alarm calls (during which time the model was hidden in the box) the sequence was repeated and the hatch of the box shut. The Training was repeated approximately 8 hrs later, with a different alarm call playback emitted from the speaker mounted on the opposite side of the aviary than for the previous Training episode.

Day 3 **Post-Training Test** (e.g., measuring trained response to the cat model)
The Post-Training Test was performed at the same time of day and in the same way as the Pre-Training Test, using either the cat model or the control object.

Day 4 **Post-Training Test** (e.g., measuring the "unlearned" response to the control)
Repeat of Day 3 using the alternate model.

The order of model presentation was randomly selected at the first age, and each subsequent presentation for an individual was alternated (e.g., if at age 1 mth the Post-Training Test model presentation order was cat then control object, then at age 2 mth the Post-Training Test order would be novel object then cat; Table VIII). After the first presentation, the cat model ceases to be novel. Therefore, subsequent Pre-Tests at different ages did not involve presentation of the control object.

Table VIII. Experiment II Training regime: showing (i) order of Testing and (ii) age at Training.

CLUTCH (number of individuals)	MODEL PRESENTATION AT DIFFERENT AGES (mth)[1]			
	1	2[2]	6	8
1 (4)	c-t-nc[3]	cn	c-t-cn	c-t-nc
2 (3)	n-t-cn	nc	c-t-nc	c-t-cn
3 (3)	n-t-nc	cn	c-t-cn	c-t-nc
4 (4)	c-t-cn	nc	c-t-nc	c-t-cn
5 (3)	c-t-nc	cn	c-t-cn	c-t-nc
6 (3)	n-t-cn	nc	c-t-nc	c-t-cn
7 (3)	n-t-nc	cn	c-t-cn	c-t-nc
8 (3)	c-t-cn	nc	c-t-nc	c-t-cn
9 (3)	c-t-nc	cn	c-t-cn	c-t-nc

[1] For ease of presentation the ages of birds are rounded to the nearest month.
[2] Recognition Test only, no Training.
[3] x-t-xy = PreTest-Training-PostTest; c=cat, n=novel control, t=Training.

All birds received the Training and Testing regime three times before they were released (Table VIII). The periods were designed to reflect key stages in wild stilts' lives. First, during the period of rapid growth as pre-fledglings (1 mth). Second, during autumn/winter, when predator densities are high and prey scarce in the wild (age 6 mths), and finally at pre-release ages equivalent to independence from family groups in the wild (8 mths).

Thirty days after the pre-fledgling Training (age 2 mths) all individuals received Recognition Tests. The Recognition Tests were conducted in the large aviaries and in the same way as the Training Tests, but consisted of 2 min model presentations on consecutive days (c.f. 3 min in Training Tests; refer p. 29).

2.3.2 Experiment II: Results

2.3.2.1 Overview of juvenile black stilts' responses to Testing

Captive-reared black stilt chicks displayed fear when a novel object (cat or control model) was introduced into their brooder enclosure. A typical response was to move away from the model while frequently stepping, head-bobbing and alert posturing (e.g. upright), with some individuals alarm calling and exhibiting escape behaviours (e.g. "walk fence"). Birds were then likely to become curious of the novel object and some approached the model.

2.3.2.2 Age: One month (brooder aviary)

Juvenile black stilts remained further away and attempted to escape more frequently in response to the cat model than for the control object (Mann-Whitney U, =0.01; Table IX; Figs 4 & 5 respectively), indicating that juvenile captive-reared black stilts recognized the cat model as more threatening than the control object upon initial exposure (i.e. a significant difference between response of juveniles to the cat and control models in the Pre-Test = PRE-TEST MODEL EFFECT,).

A TRAINING EFFECT (i.e. a significant difference in the response to the same model in the Pre-Test and Post-Test) was found in responses to the cat model. The rate of "walk-fence" escape behaviour increased (Wilcoxon, p=0.0002; Fig. 5) and the rate of head bobbing decreased (Wilcoxon, p=0.003; Table IX) in response to the cat model in Post-Training Tests relative to Pre-Training Tests. No Training effect was found for responses to the control model (Table IX). The relative behavioural differences due to Training (Post-Training Test minus Pre-Training Test response levels compared for each model) were not significantly different between the cat and control models; i.e. Training effected equivalent changes in the birds' responses to both models.

A POST-TEST MODEL EFFECT (i.e. response differences between the cat and control models in Post-Tests) was found. The birds maintained a greater distance from the cat model (Wilcoxon, $p<0.001$; Fig. 4), and showed a higher frequency of "walk-fence" behaviour (Wilcoxon, $p=0.001$; Fig. 5) than they did to the control model.

2.3.2.3 Age: Two months (large aviary). Composite Agitation Scores (CAS) for the 2 mth Recognition Test (Fig. 6) showed that the birds responded significantly more to the cat model than to the control object (MODEL EFFECT; Wilcoxon, $p<0.0001$). Higher CAS to the cat model were influenced by a higher frequency of flights (Wilcoxon, $p=0.0031$) and upright postures (Wilcoxon, $p=0.0124$), and less foraging (Wilcoxon, $p<0.0001$) than exhibited to the control (Table X).

2.3.2.4 Age: Six months (large aviary)

A TRAINING EFFECT was found in the Pre- and Post-Test CAS to the cat model at 6 mths. The birds responded less strongly to the cat model after Training than before Training (Wilcoxon, $p<0.001$; Fig. 7). Where the cat model was presented in Post-Tests, the decreased CAS were the result of lower rates of head bobs (Wilcoxon, $p=0.0001$), flights (Wilcoxon, $p=0.013$) and upright postures (Wilcoxon, $p=0.0002$), and increased levels of foraging (Wilcoxon, $p=0.0002$) relative to Pre-Test responses (Table X). There was no significant difference in CAS between Post-Tests for cat and control models (i.e. no MODEL EFFECT). However, birds maintained a greater distance (Wilcoxon, $p=0.0021$) in response to the cat, relative to the control model (Table X).

Table IX. Experiment II: Effect of antipredator-training on behaviour of captive-reared black stilt juveniles in brooder enclosures.

BEHAVIOUR[1]	PRE-TEST MODEL EFFECT[2]		TRAINING EFFECT[3]		POST-TEST MODEL EFFECT[4]		
	Pre-Test control	P[5]	Pre-Test cat	P	Post-Test cat	P	Post-Test control
Distance	2.05±0.06*	0.006	2.29±0.04	ns	2.40±0.03	0.001	2.20±0.06
Foraging	0.09±0.04	ns	0.10±0.04	ns	0.11±0.03	ns	0.15±0.03
Head bobbing	1.04±0.27	ns	1.40±0.29	0.003	0.82±0.12	ns	0.68±0.09
Stepping	3.18±0.41	ns	4.34±0.49	ns	6.19±0.62	0.011	4.63±0.54
Upright posture	0.25±0.04	ns	0.24±0.06	ns	0.20±0.02	ns	0.20±0.03
Walk fence	1.36±0.32	0.008	3.94±0.94	0.001	8.18±1.05	0.001	4.50±0.85

[1] All behaviours are defined as per Table III.
[2] Pre-Test model effect = Pre-Test differences in birds' responses to cat and control models.
[3] Training effect = Pre-Training and Post-Training test responses to the cat model.
[4] Post-Test model effect = Post-Test differences in response to both the cat and control models. All P-values for the control model were ns, and are not tabulated.
[5] All tabulated P-values are for comparisons of figures on either side of P-value column.
* Figures are mean ± standard error; n=29; all statistical analyses are Wilcoxon signed ranks tests.

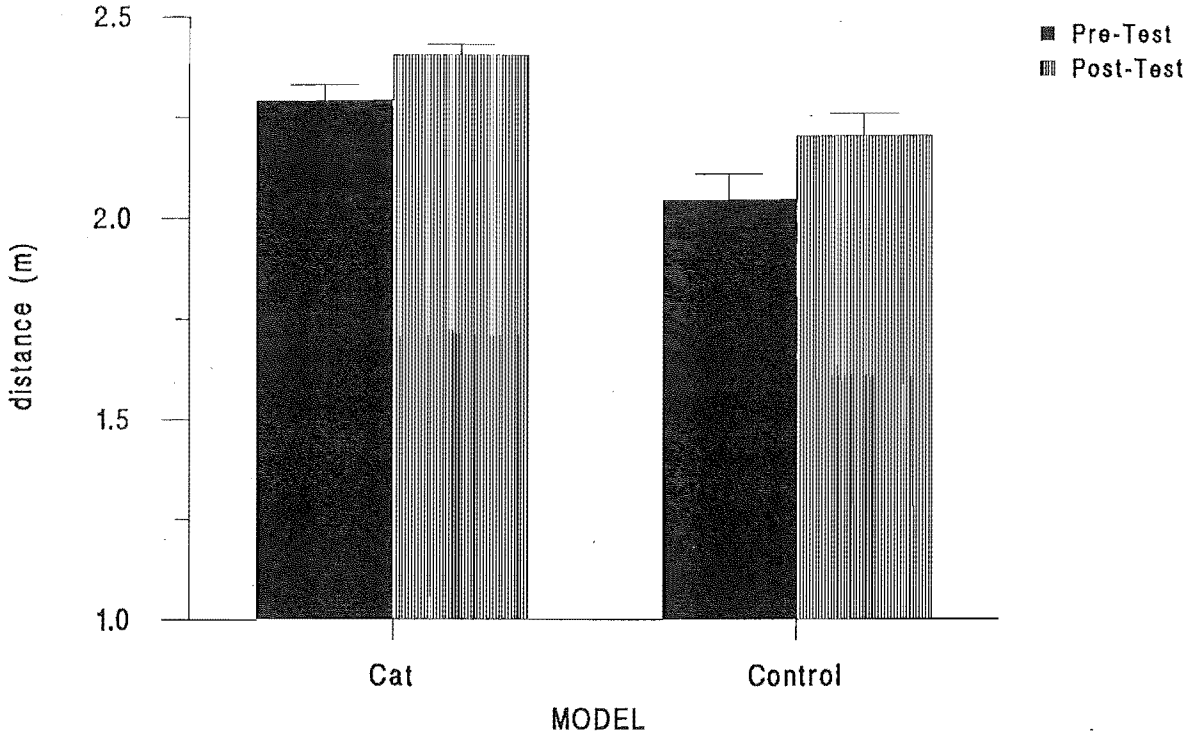

Figure 4: Experiment II: Difference between mean distance maintained from the models (cat and control) before (Pre-Test; cat, n=17; control, n=12) and after (Post-Test, n=29) antipredator-training. The maximum distance the birds could maintain from the model was 2.5 m. Pre-Test model effect = cat > control (Mann-Whitney U, p=0.006); Training effect ns; Post-Test model effect = cat > control (Wilcoxon, p<0.001). The relative difference of Training on birds' responses to the cat and control models were not significant. Mean ± standard-error bars are shown.

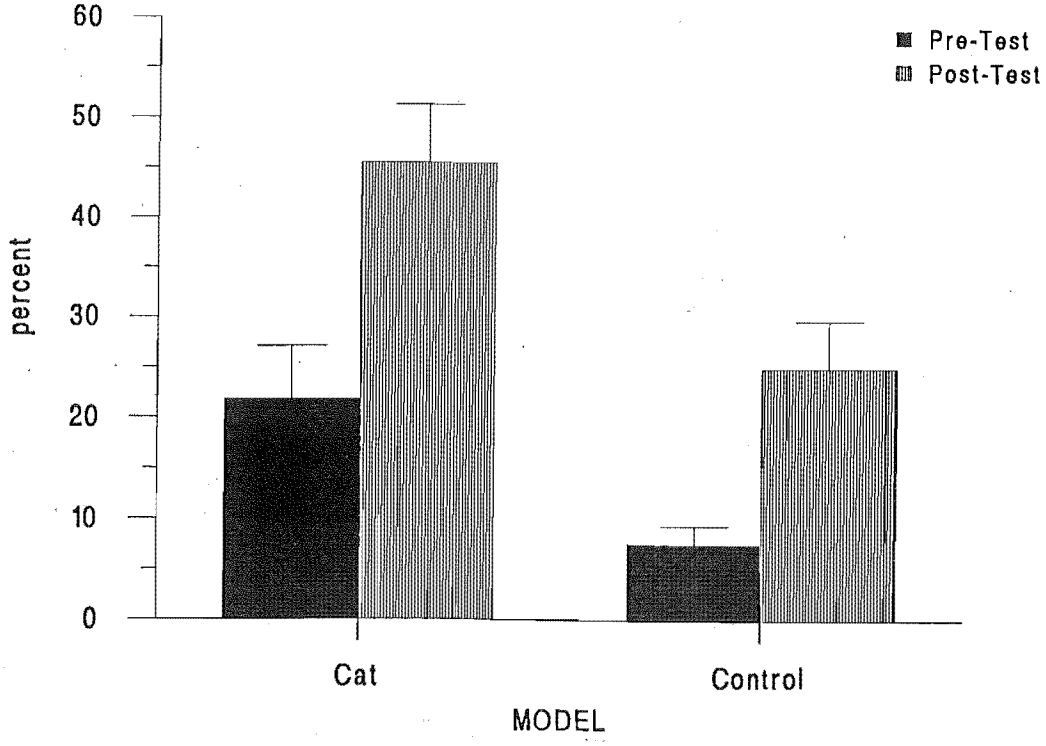

Figure 5: Experiment II: Difference between the proportion of "walk-fence" behaviour (defined in Table III) exhibited during Testing in response to the models (cat and control) before (Pre-Test; cat, n=17; control, n=12) and after (Post-Test, n=29) antipredator-training. Pre-Test model effect = cat > control (Mann-Whitney U, p=0.009); Training effect = Pre < Post (Wilcoxon, p<0.001); Post-Test model effect = cat > control (Wilcoxon, p<0.001). Percent response calculated from the proportion of the 18 observation periods within a Test that the behaviour was present. Mean ± standard-error bars are shown.

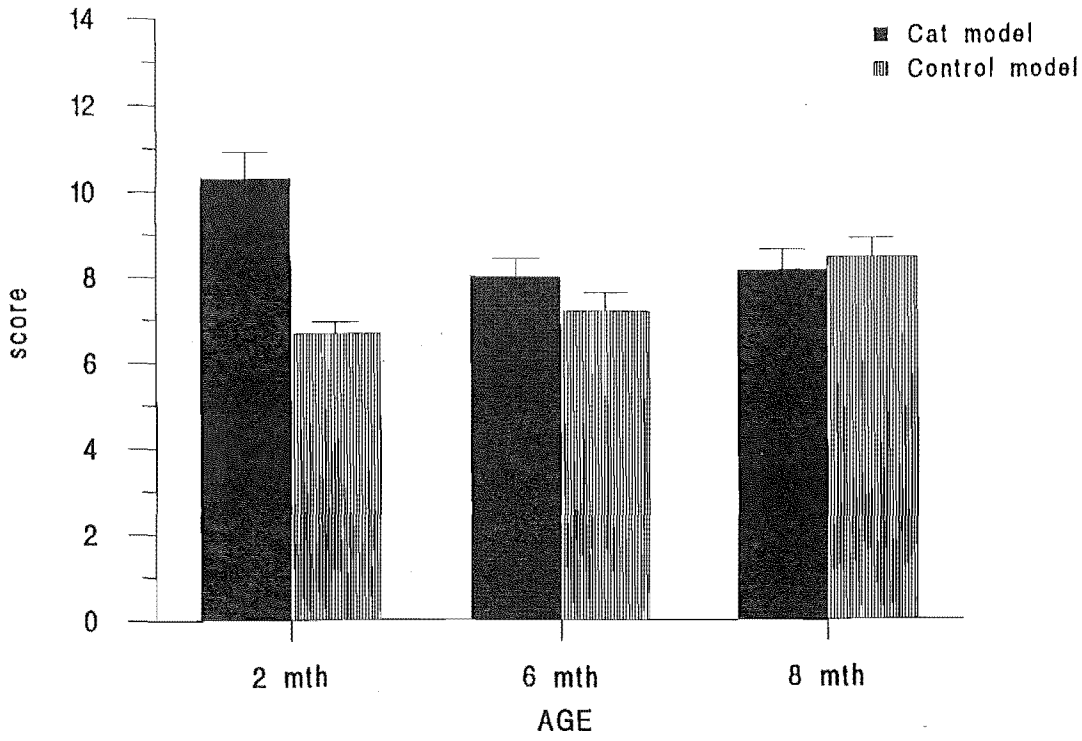

Figure 6: Experiment II: Difference between Composite Agitation Scores (CAS, defined in Table IV) in response to the models (cat and control) after antipredator-training (Post-Test responses); for the three ages of Testing conducted in the large aviaries. A model effect was found only at 2 mth (Wilcoxon, $p<0.001$). n=29 for both models at all ages; mean ± standard-error bars are shown.

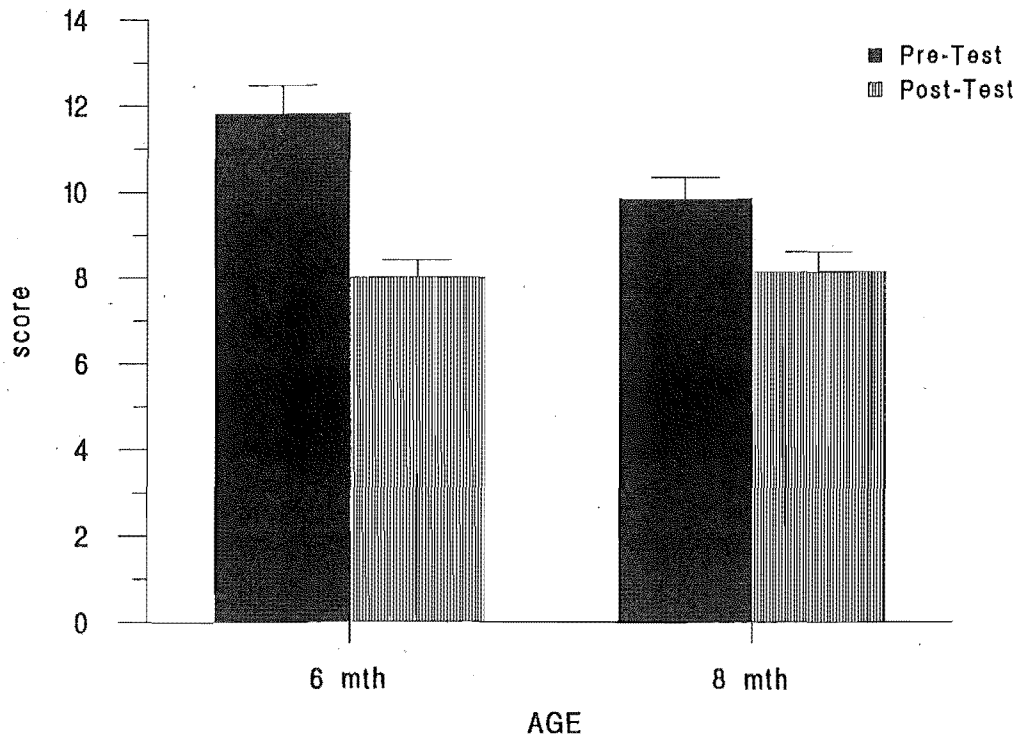

Figure 7: Experiment II: Difference between Composite Agitation Scores (CAS, defined in Table IV) prior to Training (Pre-Test) and after Training (Post-Test); for the two ages which received antipredator-training in the large aviaries. There was a Training effect at 6 mths and 9 mths (Wilcoxon, $p<0.001$). n=29 for all Tests; mean ± standard-error bars are shown.

Table X. Experiment II: Effect of antipredator-training on behaviour of captive-reared black stilt juveniles at different ages in large aviaries.

BEHAVIOUR[1]	EFFECT	AGE (mth)					
		2		6		8	
		(cat)[3]	(control)[3]	Pre[2] (cat)	Post[2] (control)	Pre (cat)	Post (control)
Composite Score	Training			12.05±1.24	8.02±0.59***	9.86±0.49	8.14±0.47***
	(Model)	10.31±0.61	6.66±0.27***	8.02±0.59	7.07±0.69	8.14±0.47	8.41±0.45
Distance	Training			4.32±0.25	4.13±0.27	4.25±0.26	4.84±0.37
	(Model)	6.90±0.80	7.42±0.79	4.13±0.27	3.34±0.25**	4.84±0.37	4.59±0.50
Foraging	Training			0.02±0.01	0.13±0.03***	0.03±0.01	0.19±0.05***
	(Model)	0.00±0.00	0.26±0.06***	0.13±0.03	0.16±0.03	0.19±0.05	0.14±0.04
Flights	Training			0.09±0.01	0.07±0.02*	0.10±0.01	0.07±0.01*
	(Model)	0.13±0.03	0.05±0.01**	0.07±0.02	0.06±0.01	0.07±0.01	0.07±0.01
Head bobs	Training			0.90±0.16	0.28±0.08***	0.53±0.12	0.21±0.05**
	(Model)	0.27±0.09	0.16±0.06	0.28±0.08	0.33±0.08	0.21±0.05	0.31±0.11
Stepping	Training			8.82±0.56	8.80±0.51	7.65±0.53	7.47±0.47
	(Model)	7.05±0.71	6.34±0.60	8.80±0.51	7.22±0.41*	7.47±0.47	6.98±0.56
Upright posture	Training			0.44±0.06	0.14±0.02***	0.27±0.03	0.17±0.03***
	(Model)	0.31±0.06	0.14±0.03*	0.14±0.02	0.12±0.02	0.17±0.03	0.23±0.03

[1] All behaviours are defined in text (Table III).

Shown are the means, standard errors and significance levels of the change in:

[2] Pre-Training and Post-Training Test responses to the cat model (Training effect; no Training at age 2 mth, Recognition Test only).

[3] Post-Test differences in response to the cat and control models (Model effect).

All statistical tests are within-age Wilcoxon signed ranks tests; where *= 0.05<p<0.01, **= p<0.01, ***= p<0.001.

2.3.2.5 Age: Eight months (large aviary).

A TRAINING EFFECT was found in the birds' CAS to Pre- and Post-Test presentations of the cat model at 8 mths. The birds responded less strongly to the cat model after Training (Wilcoxon, p=0.0016; Fig. 7). Decreased CAS were the result of lower Post-Training Test rates of head bobbing (Wilcoxon, p=0.0011), flights (Wilcoxon, p=0.0165), and upright postures (Wilcoxon, p=0.001), and increased levels of foraging (Wilcoxon, p=0.0002) relative to Pre-Training Test responses (Table X). The birds' responses did not differ between the cat and control model in Post-Tests (i.e. no MODEL EFFECT).

2.3.2.6 Training performance relates to Test performance.

The Training Response Intensity Scores (TRIS) for response during Training were related to CAS for responses during Testing at some ages (Spearman's rank, $p<0.01$; Appendix II). TRIS were significantly greater in brooder enclosures than in the large aviaries (Kruskal-Wallis p=0.0003), but were not significantly different between ages 6 and 8 mths in the large aviaries (Kruskal-Wallis, p=0.7795), indicating that behavioural responses to Training stimuli decreased between aviary types (Fig. 8; Appendix II).

2.3.2.7 Behavioural response changes over time.

RETENTION OF LEARNING was measured by comparing CAS for cat model Pre- and Post-Tests at ages 2, 6 and 8 mths (Table X). No significant difference was found between CAS for 2 mth and 6 mth Tests, indicating good retention of model recognition (Fig. 6). There was a marginally significant increase in response between the 6 mth Post-Training Test and the 8 mth Pre-Training Test (Wilcoxon, p=0.018; Fig. 7) suggesting possible habituation of responding during Training/Testing at 6 mths, and probable spontaneous recovery of responding (Chapter 3 for explanation of terms).

DIFFERENCES IN MODEL DISCRIMINATION OVER TIME were investigated by comparing the difference in Post-Test responses to both the cat and control models (i.e. Post-Training Test responses to the cat model minus Post-Test responses to the control model). There was no difference in the distinction made between models during Post-Training Tests at 6 and 8 mths (Fig. 6, Table X).

DIFFERENCES IN HABITUATION OVER TIME were examined by comparing the differences in Pre- and Post-Test CAS in response to the cat model at each age. The 6 mth difference in response was greater than the corresponding difference at 8 mths (Wilcoxon, P=0.0053; Fig. 7). The lower decrement in response at 8 mths may indicate that the birds were not habituating to the stimulus as readily at the older age, or that they have reached a minimum in responding in the Pre-Test, allowing for only minor response decrement in subsequent Post-Tests.

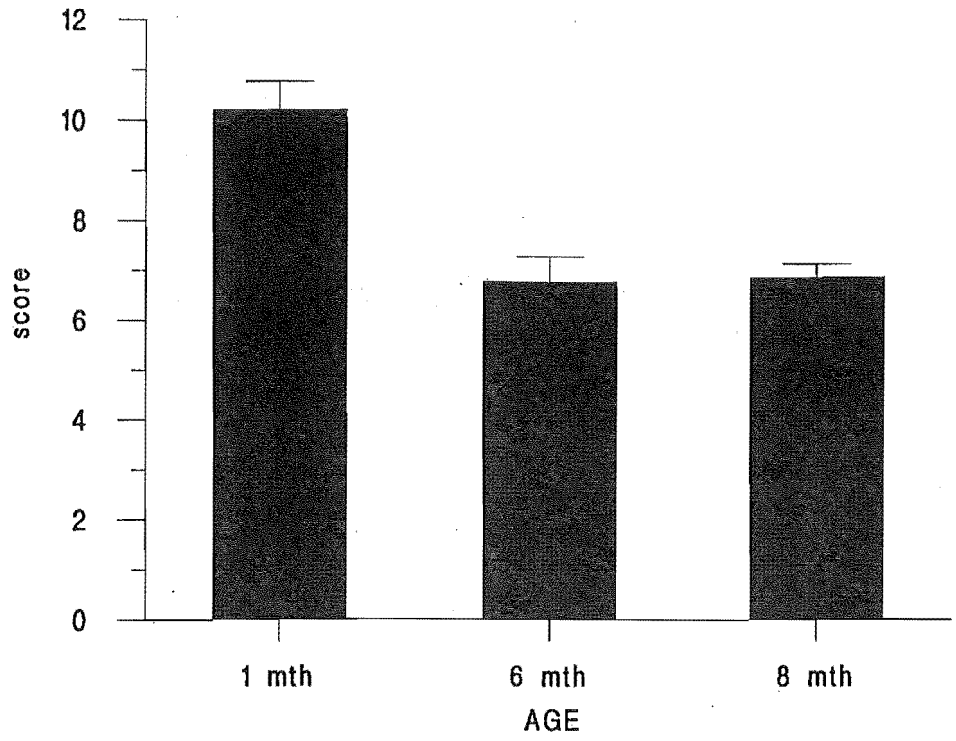

Figure 8. Experiment II: Difference between Training Response Intensity Scores (TRIS, defined in text, Table V) for the three ages which received antipredator-training. Standard error bars are shown. TRIS were significantly greater in the brooder enclosures (age 1 mth) than for responses in the large enclosures (age 6 and 8 mth) (Kruskal-Wallis, p=0.0003); there was no significant difference between TRIS at 6 and 9 mths. n=29 for all ages; mean ± standard-error bars are shown.

2.3.2.8 Effects of fixed factors.

A number of factors over which I had no control significantly influenced the birds' responses in this study (indicated by CAS, refer Appendix II). They were: clutch of placement, parent of bird, and number of animals in each clutch. Neither sex of bird, nor order of model presentation significantly affected behavioural responses during Tests.

Birds with the same PARENTAGE had more similar CAS responses than birds with different parents (Kruskal-Wallis, $p<0.01$; Appendix II). CAS were also significantly related to CLUTCH of placement at all ages (i.e. responses of individuals in the same clutch were more similar to each other than they were to responses by other birds; Kruskal-Wallis, $p<0.01$; Appendix II). Birds from larger clutches tended to respond better during Training (as indicated by TRIS), although this effect was only marginally significant (Kruskal-Wallis, 6 mths $p=0.071$, 8 mths $p=0.011$; Appendix II). A similar clutch size effect was found when the difference in birds' CAS in response to the cat model in Pre- and Post-Tests were compared (Kruskal-Wallis, 6 mths $p=0.036$, 8 mths $p=0.002$; Appendix II).

2.3.2.9 Summary of Experiment II results: Black stilt juveniles that were raised in captivity responded to their first presentation of the cat model (at 1 mth old) as more fear provoking than the control object. Antipredator-training increased some escape behaviours in response to the cat model, but not the control object; although overall, the relative change of responses after Training was not significant because responses increased to both models in Post-Tests.

Juvenile black stilts responded with greater wariness to the cat model, than to the control model in Recognition Tests one month after the first training.

Training at 6 and 8 mths decreased responding to the cat model in tests at those ages (i.e. Pre- and Post-Test comparison) and overall the birds did not respond differently to the cat and control models in Post-Tests, although they maintained a greater distance from the predator model in Post-Tests at age 6 mths.

Response intensity during Training sessions (as indicated by TRIS) was related to some of the Test responses. TRIS was greater at 1 mth in the brooder aviaries, than at any age in the large aviaries. Intensity of responding during Tests and Training, and the ability of birds to differentiate between models in Post-Tests, habituated over time.

Response to stimuli was affected by three major factors: Testing and Training being conducted in clutch groups, the number of individuals in the rearing clutch, and parentage.

Chapter 3
GENERAL DISCUSSION

The main aim of this study was to provide opportunities for captive-reared juvenile black stilts to learn about a mammalian predator that they would encounter once released into the wild. The study achieved its major aim, and showed that conditioning techniques can modify the recognition abilities of captive-reared black stilt juveniles to predator models. The success of training was shown to depend on the physical context of learning and conditioning methods used, and tends to decline in effectiveness with excess repetition (i.e. habituation occurred). Antipredator-training did not appear to increase survival of reintroduced birds within the limits of the sample sizes tested. In reality, post-release survival of Trained birds was not an appropriate measure of antipredator-training success, because of small sample sizes and non-predator causes of mortality.

Managers of captive-rearing programmes have become progressively more aware that raising animals to maturity and releasing them into the wild is not alone sufficient to ensure the continued survival of the reintroduced individuals. Managers have started actively concerned with ensuring that animals destined for release have the skills necessary to thrive in the wild. Predation is a major cause of mortality of reintroduced animals, but techniques to train captive-reared animals to cope with predators are often perceived to be difficult to design and implement. The second aim of this thesis was to determine how juvenile black stilts that have been raised in captivity could be made wary of predators prior to release. This chapter includes suggestions on how such techniques could be integrated into the existing black stilt management programme.

3.1 Baseline responding and effects of brooder aviary antipredator-Training.

The results from Experiment I indicated that antipredator-training immediately post-fledging caused increased wariness in juvenile black stilts. The distance maintained from the cat model was significantly greater in the Trained birds than for the Untrained birds. However, not all differences in behaviour could be attributed solely to Training and decreases in some alert behaviours of Trained and Untrained birds were probably due to the juvenile birds becoming used to the Testing stimuli (i.e. habituation to stimuli, resulting in response decrement or extinction of responding).

Experiment II showed that captive-reared juvenile black stilts were more fearful (as indicated by increased distance and frequency of escape behaviours) of the cat than the control model, prior to any predator experience. Antipredator-training before the juveniles have fledged increased the birds' level of wariness to both models, and Recognition tests one month after this Training showed that the black stilts responded with significantly more caution to the cat model than to the control model.

Naive animals have been found to be initially cautious when presented with a novel object, but show even greater fear of predator models (Curio 1975; Curio et al. 1978; Morse 1980; Mueller & Parker 1980; Sordahl 1980; Pitcher 1986; McLean et al. in press). For example, minnows (*Phoxinus*) from a population that have lived without pike (*Esox lucius*, a major predator) for many thousands of years, are capable of performing synchronized antipredator behaviours in their first encounter with a pike (Pitcher 1986). Recognition of cat models as dangerous by naive black stilt juveniles implies two things. First, that the cat model is perceived to represent the dangers of a live cat, and second, that such recognition may have some genetic basis. The background to the role of genetics in mammalian predator recognition in black stilts may be explained by three hypotheses. First, genetic recognition of mammalian predators may be a remnant of the Australian ancestors of black stilts, who would presumably have been prey for a number of mammalian predators, including the thylacine (*Thylacinus cynocephalus*), native cats (*Dasyurus sp*) and dingos (McLean et al. in press). Second, the recognition of the cat model as dangerous could mean that black stilts' exposure to extreme predation pressure from cats in the past 150 years has been sufficient to select for individuals that recognise cats as dangerous (Maloney

pers. comm). When environmental conditions change rapidly, both genetic and traditional (i.e. resulting from learning) inheritance of information can lead to a time-lag during which the population is essentially locked into unadaptive old ways by phenotypic or acquired traits. During this time-lag, the change in the environment reduces the fitness of individuals in the population, and the population may become endangered or go extinct. Natural selection continues to favour those individuals in an endangered population who acquire traits that increase fitness in the new environment (Temple 1978). Perhaps this process induced changes in the black stilt population, and remaining individuals have superior predator recognition skills. Finally, McLean et al. (in press) propose that naturally cautious animals may react even more cautiously to an animal larger than themselves, than they would to an inanimate strange object. Black stilts are a generally cautious species (i.e. aware of their surroundings and easily roused to flight by disturbance, or alarm calls of other birds that may indicate possible disturbance; pers. obs.) and perhaps the initial widespread fear of novel objects may have provided the baseline upon which a tradition of enemy recognition has been built (Wilson et al. 1994).

Irrespective of the relative contributions of genetic or learned knowledge, this study showed that pre-fledging (i.e. less than 1 mth) antipredator-training increased both the birds' level of wariness of the cat model, and the birds' ability to differentiate between the threatening cat model and the benign control object for up to one month after the first Training (as indicated in the Recognition Tests).

3.2 Response intensity during Training affects Test behaviour.

The results of Experiment II agree with previous studies that have found that an animal's performance during Training affects the efficacy of learning and subsequent Post-Test responses (Vieth et al. 1980; with blackbirds, *Turdus merula*). For example, high intensity responses during Training are related to better responses during Testing. The predictable nature of responding could be useful in black stilt management, where birds' readiness for release could be established by performance in Training episodes.

3.3 Decrement in responding does not necessarily represent decreased recognition.

Antipredator-training of juvenile black stilts when they are approximately 1 mth old increased their wariness to both the cat and control models; and testing of model recognition 1 mth after the first Training (i.e. in the 2 mth Recognition Test) indicated that the trained birds were significantly more wary of the cat model than they were of the control. However, data from Tests at 6 and 8 mths indicated that the juveniles were becoming progressively more complacent about the possible threat of the cat model. This complacency was obvious in both the decrease of the conditioned response to the cat model, and the decreasing tendency of the birds to respond differentially to the cat and control models. Probable explanations for the decrement in alert and escape behaviour in response to the models include habituation, aspects of the experimental design (i.e. inadequate conditioning stimuli or procedures) and limitation on my ability to validly measure responses. In the following sections I will examine habituation as my preferred explanation for the decrement in responding; and also consider alternative interpretations for the decrease in response intensity over time.

3.3.1 Habituation

Habituation is the waning of response as a result of repeated or continuous stimulation that is not followed by any kind of reinforcement (Shalter 1984), and is a basic process found at all phylogenetic levels (Kimble 1961). The theory of habituation predicts that a novel stimulus which initially causes a reaction (e.g. wariness, fear), but results in no negative consequences, will subsequently tend to be treated as safe and responding will decrease (Hinde 1970). An important function of habituation is to allow animals to save energy by discriminating between dangerous and harmless objects and situations.

The idea that an "unpleasant" experience with a stimulus will intensify an initial fear reaction (i.e. conditioning), while indifferent experience will weaken the reaction (i.e. habituation) has been noted by a number of researchers (Hertz 1926; Nice & ter Pelkwyk 1941; Magurran & Girling 1986; Järvi & Uglem 1993). My study used the pairing of an "unpleasant" experience (US=alarm calls) with a cat model (CS), to

condition a fear of cats. However, the weakening of response due to habituation is in direct competition with the desired outcome of conditioning. A clear way to minimize habituation is to ensure that the "unpleasant" stimulus is as intense, noxious and variable as possible. Such techniques are discussed in the following Management section.

Habituation was not detected in the brooder aviaries, but was apparent in the large aviaries. Variation of habituation in different aviary types could be due to an increase in the ability of animals to assess risk as they age (Miller et al. 1990). Black stilts may regulate their antipredator responses to stimuli (and therefore the observer's judgement of recognition) based on perceived danger. For example, a feeding black stilt may see a predator in the distance and continue to feed; but if that predator was closer or behaving in a threatening manner, the black stilt may perceive itself to be in more danger and subsequently preform escape behaviours. The degree of danger posed to the bird can be thought of as a continuum, the endpoints being the situation in which the prey is safest from the predator, and the point at which the prey is killed by the predator (Fanselow & Lester 1988). Fanselow & Lester (1988) hypothesize that both qualitative and quantitative changes in defensive behaviour occur as a function of the prey's perception of where it is on this continuum. This continuum is referred to as one of "predatory imminence" because it reflects both physical (how far away the predator is) and psychological distance (based on the predator's behaviour; e.g., a stalking animal is more of a potential threat than a wandering predator). I hypothesise that the presentation of the cat model and alarm calls in the brooder aviaries would make the Training experience very intense because of the small ground area (3m x 2m); whereas the area of the large aviaries (14m x 7m) would mean that the intensity of Training was "diluted". Juvenile black stilts may perceive the danger of the Training situation in the large aviaries to be less than the danger in the brooder enclosures. A lower perception of danger may be because the maximum possible escape distance in the large aviary enclosures is almost six times that possible in the brooder enclosures. A low perception of danger evokes a low antipredator response. Various studies have reinforced the idea that animals' interactions with enemies involve assessment as well as recognition and response (Robinson 1980; MacWhirter 1992).

The nature of the conditioning stimulus may also influence the birds's perception of danger, and subsequently the habituation rate of their response. Models have been

fatal. Conditioned responding transfers well across contexts (Whitlow & Wagner 1984), and is often unaffected by long retention intervals, whereas extinction of response is prone to spontaneous recovery in different contexts and over time (Bouton & Bolles 1979).

The properties of habituation imply certain conclusions for this study. First, the existence of spontaneous recovery shows that black stilts may still recognize the cat model as dangerous because the initial association returns, even if habituation has occurred. Spontaneous recovery also occurs for the responses to the control model, therefore the possible recovery of learned responses does not seem to differentiate between models. Although habituation and extinction appear to occur in the antipredator-training of black stilts, the properties of these processes encourage optimism in the maintenance of the birds' conditioned responding. Habituation of responding is likely to disappear with the extreme context change upon release into the wild, whereas learned recognition should persist.

When examining the decrease in responding by black stilt juveniles over time, it is important to remember a number of points. First, habituation is demonstrated in responses measured within experiments, and does not necessarily indicate a problem with the recognition of the cat. It may be that the cat model is no longer perceived as a threat in the aviary context. Second, habituation is sensitive to changes in context, while conditioned responding is not; so the increased recognition skills gained during antipredator-training may still prove useful post-release, while habituation may extinguish. Finally, habituation in these experiments was partly an artifact of the Testing protocol. It was necessary to include a Testing regime in this study to illustrate the change in response to the cat model due to Training. Testing involved presenting models in a benign manner to test behavioural response. In fact, Testing of response represented the majority of the time invested in conducting both experiments (i.e. Testing occurred on two of the three days of manipulation in Experiment I and three of four days in Experiment II). I emphasize that antipredator-training as part of a management strategy would not routinely include such Testing procedures, and therefore, the chances of habituation occurring would be greatly decreased. Suggested training regimes are discussed in the following Management section, all aim to avoid or minimize habituation.

3.3.2 Problems with experimental design.

Although I have concentrated on habituation as an explanation for the decrement in responding over time within this study, other interpretations of results are possible. The decline in response could be explained as an artifact of the experimental design. For example, an inappropriate control model in Experiment II would not reveal a possible difference in the recognition of the predator and non-predator models. Therefore, even if antipredator-training was successful in teaching predator model recognition, such recognition would be difficult to detect (discussion of the choice of control model is in Appendix I). A second explanation may be that merely presenting the cat model during Testing could provide sufficient stimulus to initiate recognition of the cat model as dangerous. If this explanation is correct, little difference in responding would be expected between Trained and Untrained birds in Experiment I. Perhaps the predator model used in the experiments, and its method of presentation, did not provide the type of stimulus I had hoped for. Researchers have found that animals respond differently to stimuli that they consider predators and non-predators, to predators that hunt differently, and to contextually different interactions with the same predator (Robinson 1980). Perhaps the behavioural responses of the juvenile black stilts were influenced by the birds' perception of risk based on the way the cat model moved and by the context of Training and Testing. There is clearly a need for more research into the possible problems associated with stimulus presentation and experimental design.

3.3.3 Difficulties in measuring responses.

A more complicated explanation for the response decrement found in this study could be my inability to accurately measure the magnitude of the juveniles' responses.

Learning is an enduring change in the neural mechanisms of behaviour that results from experience with environmental events (Domjan & Burkhard 1982). We often do not observe the critical neural processes directly, but infer that learning has occurred by observing the subject's behaviour. A response that is measurable within the constraints of the experimental design must be defined; however, the behaviour of organisms does not always reflect what they have learned (Domjan & Burkhard 1982).

The measurement of behavioural response is generally at a relatively gross level (e.g., number of alarm calls) for field biologists, and many subtleties in behaviour can be lost or ignored (McLean & Rhodes 1991).

When examining the recognition of predators, fear is the response of interest. However, fear is unobservable and the measurement of recognition is indirect. Therefore, complications may occur in the interpretation of experimental results. Observable fear responses include the prey animal attacking the predator (i.e. mobbing) or performing overtly defensive behaviour (e.g., fleeing or hiding). However, the prey animal may perform behaviour patterns that differ from undisturbed behaviour, but which seem to be neither directly defensive nor aggressive (e.g., attention postures). Or the predator could ignore the predator and not alter its behaviour (Smith & Smith 1989). Neither of these responses would be interpreted as fear or recognition in behavioural experiments. Perhaps black stilt juveniles were responding to the model stimuli in ways that were unable to be detected using my methodology.

Juvenile black stilts could respond in a number of potentially equivalent, but different, ways to the stimuli (e.g., flying or running away are both appropriate responses to a predator). Variation of responding across behavioural measures could affect the conclusions drawn by the observer. For example, during a Test a bird may respond to the predator appropriately by flying, or running, but not both. Then for analyses on flying or running conducted separately, the flying individual enters the "running" analysis as a zero, and vice versa. Although equivalent with respect to the overall Test results, variability in responses increases the variability in each behavioural measure. Even when tests are conducted under identical conditions, within-species variation may range from no visible response to extreme mobbing involving physical attack and loud continuous alarm calling (Arnold & Bennett 1984; McLean & Rhodes 1991). Variance in measurable responses may be due to erratic behavioural responses, or different responses being equally effective (McLean & Rhodes 1991). Therefore, difficulties arise for a researcher attempting to find a meaningful variable to measure overall behavioural change. Such a response variable must take into account individual variability and the different implications of responding in certain ways. In general, defensive behaviours cannot be substituted for one another, and no one defensive behaviour can be used to represent the entire response of all subjects (Blanchard & Blanchard 1990).

To cope with an entire system of responses, some researchers have developed species specific composite variables of responding (Giles and Huntingford 1984; Maloney 1991). Composite variables generally have positive loadings for antipredator behaviour and negative loadings for non-appropriate behaviours (e.g., feeding, grooming). I developed a Composite Score of general Agitation for use with captive black stilt responses. By using the Composite Agitation Score (CAS), I was able to measure the general levels of response more accurately than if I merely relied on the change in response levels of each behavioural measure. The response of juvenile black stilts' in the behavioural categories used to make up the CAS were consistent with the birds' overall Composite Score. For example, cases where the CAS during a Test was relatively low generally indicated high frequencies of not fearful and negatively loaded activities (e.g., feeding, preening and close proximity in response to the models) and low frequency of fear and escape behaviours. The CAS attempts to identify the overall response by compensating for variation in a number of behavioural measures.

The black stilt data showed notable internal consistency of exhibited motivation (i.e. fear, or no fear) in the black stilt data, and therefore within the Composite Score; I consider that the measurement techniques used in this study provided data that accurately represented the birds' responses. However, the precise magnitude of response, or fine scale difference, may have been lost in the sampling and measuring techniques. Problems of this sort are normally dealt with by increasing sample sizes, which was not an available option in this study. Each year approximately 30 birds were reared in captivity and available for me to Train.

3.4 Methodological Constraints: Their presence and implications

During the course of this study a number of unanticipated, yet consistent, sources of uncontrolled variation, including loss of variance due to correlated responses between individuals, became apparent. Differences in the birds' behavioural responses were found to be related to clutch (i.e. due to birds being tested in groups, and the number in the clutch) and parentage, but not order of model presentation or sex of bird. Such sources of variation consistently pervade not only the initial intensity of response, but also the extent and rate of learning and habituation by each individual.

I attempted to minimize the effects of extraneous variables by keeping constant all factors under my control (e.g., time of day of Training and Testing, stimulus and stimulus presentation); however, the existing management programme necessarily restricted my manipulation of some factors. For example, I was unable to dictate which individuals were raised together (i.e. siblings or individuals from a number of parents), how many individuals were in each clutch, or precisely where each clutch was housed in the aviary space; nor could I test individuals separately. Such factors were found to have significant effects on behavioural responses.

3.4.1 Sources and Functions of Variability.

In addition to individual variation, responses of animals can vary with season, dominance status, group size, group composition, environmental factors, age, sex, behaviour of the enemy, previous experience an a host of other factors (review in Montgomerie & Weatherhead 1988).

The presence of clutch differences in habituation rates (also found for neonatal garter snakes, *Thamnophis spp*, Herzog et al. 1989) as well as large individual differences (also found in domestic fowl, *Gallus gallus domesticus*, by Shalter 1975, 1977; and pied flycatcher, *Ficedula hypoleuca*, Shalter 1978) of newborn animals reared and tested under controlled conditions suggests significant genetic contributions to learning and habituation. Some animals consistently differ in general anxiety/timidity (Wilson et al. 1994), and in their ability to cope with environmental events (e.g., three-spined stickleback, *Gasterosteus aculeatus,* in Huntingford & Giles 1987). Individuals have been found to be consistent in their responses when retested at relatively lengthy intervals (Herzog et al. 1989). This study also showed that individuals are consistent in their responses. For example, birds that exhibit wary responses to the cat model in the Recognition Test (at 2 mths), were likely to be better responders at 6 and 9 mths also. Consistency in responding may indicate a genetic base to recognition learning and it may be possible to breed only from those parents who consistently produce wary offspring. Selective breeding would make the assessment of individual variability, including variation in learning processes, useful in a captive-rearing context.

An animal's ability to habituate to repeated stimulus presentations may be

adaptive under many circumstances. For example, the ability of some species of bird (e.g., crows) to habituate to scarecrows or crop-protection detonators has long aggravated crop farmers, but is clearly advantageous for foraging behaviour in the birds (Bondreau 1968; Conover 1985). The existence of large and apparently genetically-based individual and clutch variation in juveniles raises a number of interesting questions that can only be answered by further research. For example, my experiments clearly demonstrated that habituation of antipredator behaviour can occur in controlled situations. However, further work is needed to show how this process operates in confrontations with actual predators and in the wild environment. One conclusion that could be drawn from the presence of response variability within the captive black stilt population is that no one pattern or level of antipredator response is sufficiently adaptive to become fixed. In fact, it is possible that variable, erratic, or unpredictable antipredator responses are conducive to the survival of some offspring. The maintenance of high levels of variability might be particularly important where the kind and intensity of predation can vary from year to year. This study, and those of others (Shalter 1978; Herzog et al. 1989), indicate that individual experiential effects can occur and interact with genetic variability; and such variation could prove beneficial for the animal. However, if variation in responding is beneficial for the survival of individuals, statistical analysis of results of studies such as this will be difficult. In extreme cases statistical analyses may be inappropriate as they may obscure, not highlight, features of biological significance (McLean & Rhodes 1991). However, there are solutions if the problem can be recognised *a priori* (McLean pers. comm.).

3.4.2 Response to Stimuli is Influenced by Treatment in Groups.

Birds are often social animals, both in the family and in the flock, and it is to be expected that the behaviour of one individual would be influenced by the behaviours of others without necessarily involving imitation (Thorpe 1951; Curio et al. 1978). Various observations support the idea that the social and emotional climate of a group is important in facilitating and/or inhibiting individual behaviour (Lorenz 1931 cited in Curio 1978; Box 1984). Fear of an animal model can be learned if a trainee bird witnesses other birds mob the model. The trained bird will then avoid or mob the

model later (Marler 1956; Marler & Hamilton 1966; Stefanski & Falls 1972; Curio et al. 1978).

The most common social bond is between parent and young, and rapid development of adult-like responses in a species with extended semi-dependence may occur as a consequence of observational learning (Cully & Ligon 1976). Parent-to-offspring transmission of information about predators may be an important function of the family group in black stilts, as has been found in juveniles of other Recurvirostridae species (by Sordahl 1980 in american avocets, *Recurvirostra americana*, and black-necked stilts, *Himantopus mexicanus*) and should be facilitated by the long period of semi-dependency in this species (Cully & Ligon 1976; Stamps 1991).

This present study found a strong effect of clutch throughout the results, i.e. behavioural responses of birds in the same clutch were more similar than those of birds in different clutches. Problems of independence of responses were introduced because response variability was greater between clutches than between individuals within the clutch. However, in the context of predator recognition, I consider the biological significance of group learning to be more important than statistical independence. The potential positive effects of social facilitation for antipredator-training are discussed in the following section on management issues (section 3.5.3).

Behavioral imitation could be described as "social learning" and social facilitation could be described as "contagious behaviour", where the performance of a general instinctive pattern of behaviour by one member of the flock will tend to act as a releaser for the same behaviour in others (Thorpe 1951). Social facilitation could explain the clutch effects in this study and may confer strength to the Training stimulus by way of social learning. Anything that makes the Training experience more intense for the birds is beneficial. For example, if seeing other birds respond to a stimulus with alarm makes a bird alarmed also, then the contagious behaviour effect potentially increases the strength of antipredator-training. If the contagious behaviour concept operates in this way, it could be used to predict that birds from larger clutches would have relatively greater responses than those in smaller clutch groups. The findings of this study support this prediction; birds in clutches of four showed significantly greater Training and Testing alarm and wariness, compared to clutches of two and three.

3.5 Management Issues

3.5.1 Existing skills of captive-reared animals

Innate expression of predator avoidance varies from species to species. Consequently, the type and amount of pre-release preparation necessary to enhance the probability of successfully reintroducing captive-raised animals into the wild will also vary (Kleiman 1989). Some species may retain innate antipredator behaviours in the absence of predatory pressures, whereas other species undergo erosion of those traits when selective pressures are relaxed. The complex interaction between innate and learned responses will be altered by captivity (Miller et al. 1990). Information gathered during this study indicates that black stilts lie somewhere between the two ends of the scale. For example, juvenile black stilts can recognise the cat model upon first exposure indicating some innate knowledge; but the captive environment does not provide opportunities to improve antipredator skills with practice, and such skills may degrade with time in captivity.

3.5.2 Using limited stress to prepare captive-reared animals for the wild

Managers of most captive-rearing programmes (and the black stilt programme is no exception) attempt to maintain excellent standards of animal welfare, and this usually includes keeping stress to a minimum (Kleiman et al. 1991). The basic feeling is that stress is negative and in a general sense this is correct; none of us likes to think of animals subjected to stress. And an overly stressful rearing environment can produce substandard animals, which are unlikely to survive in the wild (Reed pers. comm.). However, in measuring the welfare of captive species, managers use two contradictory criteria. First, it is assumed that lower levels of stress result in greater animal well-being. It is also assumed that a more natural environment results in improved well-being. Yet, in the real world, the natural environment is stressful, including such things as periodic food and water deprivation, exposure to climatic extremes, potentially fatal social conflict and exposure to predators, parasites and disease (Kleiman et al. 1991). In fact, experience of unsuitably low levels of stress during rearing could be interpreted as detrimental to birds' survival once released into

a stressful natural environment. Interactions with predators are both a natural cause of stress, and an important part of the wild environment. If captive-reared animals are to be trained to recognise predators that they will encounter after reintroduction, I believe that a little controlled stress during antipredator-training is desirable and could help avert death by predation post-release.

3.5.3 Observations as a result of this study

A comparison of different possible training techniques could not be attempted in my study because of methodological consistency and limited sample size. However, I believe that the information I have gained, and that of other researchers, can lead to the development of practical training programmes. I consider there to be better ways to teach antipredator skills than the training methods used in this study. The experimental methodology used in Experiments I and II was constrained by the need to maximise sample size and maintain consistency in Training and Testing. Any future training regime might not require testing to be a regular part of the methodology (therefore minimizing habituation), and need not involve separating the birds with screens. By removing the screens, and having the stimuli witnessed by a number of birds which can also observe each other, I suggest that the juveniles would benefit from observational and social facilitation of learning during Training; thus making living and Training in groups advantageous for reinforcement of response. For example, studies have found that selective responding by adults helps to speed juvenile recognition of predators and non-predators (Nice & ter Pelwyk 1941 in song sparrow; and Seyfarth & Cheney 1986 in vervet monkeys, *Cercopithecus aethiops*).

In species where juveniles remain with their parents for an extended period, the effects of parental behaviour on offspring fitness are likely to be strong (Stamps 1991), and the role of learning especially important. Black stilt juveniles have a long semi-dependence period and given the length of time they remain with their parents, I hypothesised that learning would occur over a protracted period, rather than a small critical window of time. I chose to conduct repeated Training episodes at a number of ages. The results gained from Experiment II indicate that such extended training may not have been necessary, and that fewer Training events could be more effective by minimizing the chance of habituation to the Training stimuli. Other researchers have

found similar results, and often one brief simulated predator experience (Hinde 1954 cited in Peeke and Herz 1973; Magurran 1990), even one relatively benign presentation of a predator (Ginetz & Larkin 1976; Blanchard & Blanchard 1989; Maloney & McLean in press), is enough to influence defensive behaviour, and in some cases produce long-lasting effects.

Details of sensitive periods in the development of black stilts are unknown. However, the knowledge gained from this and other studies of stilts (Sordahl 1980), indicates that one or two antipredator-training events timed for pre-fledging (<35 days) and pre-release (8-9 mths) would probably be most effective. During fledging, chicks observe their parents' reaction to a number of predators and non-predators each day (Sordahl 1980), hence are expected to be especially receptive to learning at fledging age. This study showed that there appears to be both an increase in the general wariness of black stilts, and a decrease in decrement of response due to Training occurs at 8 mths of age, just prior to the birds' release. Age-related changes in response pre-release could indicate a maturation of a general wariness characteristic, which would correspond to the age when juveniles would be reaching independence in the wild. Therefore, a Training experience at 8 mths would maximise the influence of any natural increase in wariness and provide a reminder of the danger of mammalian predators immediately prior to release.

Once the timing of events has been established, the next important detail is the number of Training events necessary for conditioning of response. Repetition is usually seen as a basis for habituation but, within limits, repeated presentation of stimuli can be informative and augment responses (Beer 1973; Shalter 1974 cited in Shalter 1984). Although the rates of habituation, learning and forgetting vary interspecifically, findings from previous research can provide useful insight into the learning process. One or two intense stimulus episodes of medium duration (i.e. a few minutes) provide the best learned responses, minimize habituation (Hurley & Hartline 1974; Magurran & Girling 1986) and persist for longer (Mineka & Cook 1993). It has been suggested that learning, for rhesus monkeys (*Macaca mulatta*) that witness a live conspecific model behaving fearfully with snakes, may be asymptotic or close to asymptotic after two sessions of observational conditioning (Mineka & Cook 1993).

In summary, to train captive-reared black stilt juveniles to be wary of mammalian predators, I recommend one or two training stimulus presentations to groups of birds, of a few minutes duration, when the birds are approximately at fledging age.

Presentation should be repeated immediately prior to release of black stilts into the wild.

I would like to emphasize the preliminary nature of the conclusions drawn from this study. Clearly, more research is necessary to *quantitatively demonstrate* the worth of investing energy in antipredator-training black stilt juveniles for life in the wild. However, I believe that antipredator-training has the potential to *qualitatively* improve the captive-rearing environment for juvenile black stilts. Part of the black stilt management directive has involved targeting ways to make the captive-rearing environment more natural, and therefore more likely to produce juveniles that will survive in the wild (Pierce 1980; Reed et al 1993). I consider that antipredator-training has the potential to increase the survival of reintroduced black stilts as much as any other rearing practice currently used to prepare the birds for the wild environment (e.g., providing realistic foraging environments). The following recommendations should be considered as offering plausible suggestions about how to prepare black stilt juveniles that are raised in captivity to enhance their chances of surviving when reintroduced into the wild environment.

3.6 Suggestions for using Antipredator-training to Prepare Black Stilt Juveniles for Reintroduction.

I suggest four possible methods for antipredator-training of captive-reared black stilts. The first technique is perhaps the most frightening (and potentially the most potent) for the birds and involves black stilt juveniles watching another bird interact with a live predator. My second suggestion involves the interactive, but non-contact, use of a predator. This is probably not as frightening as contact training, but may be preferable for ethical and practical reasons. The third suggestion is to antipredator-train black stilts immediately post-release, when the birds are in a more natural setting. The first three ideas involve antipredator-training of juveniles using conditioning with models. My final suggestion is to rear black stilt juveniles with a surrogate parent to give them opportunities to learn from a live "parent".

All training suggestions fulfil the three important criteria for an effective antipredator-training regime, as itemised by Maloney (1991):

1. Training must keep the attention of trainees for as long as possible.
2. Training stimuli and regime should reflect a life-like situation so that the trainees are likely to associate the regime with realistic enemy encounters.
3. The training event should be effectively focused on the object of training (i.e. on the enemy stimulus).

3.6.1 Learning about Predators by Observation of Direct Predator/Prey Confrontations.

Animals are well known to learn by observation (Klopfer, 1957; Kruuk 1976; Curio et al. 1978; Mineka & Cook 1993). The three latter papers reported that the birds were able to learn to avoid potential enemies by witnessing an encounter between conspecific and predator. The methods I propose for antipredator-training of black stilts are necessarily frightening. A frightened animal experiences a degree of stress, and certain amounts of stress make for effective learning. Clearly excessive stress can be detrimental, and in some cases counter-productive. For example, tonic immobility in response to the type of excessive stress caused by a surprise predator attack may not be conducive to learning about that predator. A practical example of how predator training can improve the antipredator behaviour of a captive-reared species is provided by Järvi & Uglem's (1993) predator training study of hatchery reared Atlantic salmon (*Salmo salar*) smolt. Researchers used both contact training (where the smolt experienced free hunting cod predators, *Gadus morhua*), and non-contact training (where the smolt experienced the predator from behind a transparent partition). It was found that predator training improved the antipredator behaviour of the smolt, although the two training methods showed different effects. Smolt learned and responded better as a result of the more stressful training (i.e. smolt exposure to a free hunting predator).

By combining the knowledge that animals learn by observation, and that training animals to recognise predators as threatening is most effective when a particularly distressing US is used in tandem with a realistic CS. I suggest constructing a confronting Training experience in which black stilt juveniles witness a conspecific interact with a live predator (e.g., cat, mustelid, harrier). An appropriate prey stimulus

could be a pied stilt, or even any other bird species (e.g., bantam, especially if Suggestion 4 is adopted; see section 3.6.4). Irrespective of which bird species is chosen, the important components of the Training event would be equivalent (i.e. the predator attacks the bird and is perceived as dangerous).

I appreciate that such an intrusive option may not be ethically or practically acceptable. Issues involved in live predator/prey interactions are ethically complicated (Huntingford 1984), although live animals have been profitably used in predator experiments elsewhere (e.g., Conover & Perito 1981). Aiding the continued survival of an endangered species might be seen as sufficient reason for implementing what are sacrificial methods. Some ethical concerns could be avoided if the "prey" was killed ahead of time. However, the use of a dead prey and a living predator (or predator model) confers no advantage over using the predator alone (Conover & Perito 1981; Maloney 1991). For example, Conover & Perito (1981) found that starlings (*Sturnus vulgaris*) were more wary of an owl model after a live starling was tethered to its talons, than they had been during presentation of either stimulus separately, or of the first presentation of the owl. Therefore, using a dead prey in antipredator-training might not be as effective as live prey. Both cases involve death of the prey and it seems appropriate to make most efficient use of the death of the prey animal. By using live predator and prey animals, the strength and impact of the Training event would be maximised.

I consider it necessary to use the most intense training stimulus as possible. When the Training stimulus is as noxious as possible, a single exposure may be sufficient to cause significantly increased response to predators (Ginetz & Larkin 1978; Magurran 1990; Chivers & Smith 1994). The benefits of observing a live predator/prey interaction include realistic representation of the predator (c.f. predator model), appropriate alarm calls and behaviour from the prey (c.f. recorded calls) given in response to genuine fear, and response action and counteraction of predator and prey so that the contingency of behaviour is clear. An additional benefit is that birds in a number of aviary enclosures could witness the Training event at once, therefore the learning process could be aided by observational learning and social facilitation.

3.6.2 Learning About Predators by Non-Contact Predator/Prey Interactions

If a direct predator/prey training situation is unacceptable, I suggest a non-contact alternative. Animals respond more strongly to live predators (Pitcher et al. 1983; Magurran & Girling 1986; Miller et al. 1990) and take longer to habituate to live animals than to models (Shalter 1978). Thus using a live predator (or realistic moving model) is preferable to a standard inanimate model.

Learning about predators is possible by using interactive non-contact predator interactions (Ellis et al. 1977; Järvi & Uglem 1993). For example, the responses of avocets and stilts to terrestrial predators (skunks, weasels, foxes, and dogs) were weak, but became much stronger if the bird was then chased by a dog (Sordahl 1981). Learning about a stimulus can be increased, and the probability of habituation to a stimulus lessened, if realistic predator models are used (Nice & ter Pelwyk 1941; Shalter 1978; Magurran & Girling 1986), and the presentation time and site of the predator-dummy is varied (Schleidt et al. 1983; Shalter 1975). What stimulates animals is change, and responses are diminished by persistent repetition (Hartshorne 1956 cited in Shalter 1975). The wild environment is dynamic and constantly changing, and the relative lack of response decrement to both recurring predators and alarm communication in nature is due to the spatial and temporal novelty of the stimulus (Shalter 1975).

I propose that a practical method to train captive-reared juvenile black stilts would be to use a live predator (e.g. cat, stoat *Mustela erminea*, ferret *M. putorius*) which could move through the aviaries, but would be unable to directly contact any birds. Non-contact interaction could be achieved by using a clear perspex-type tube that is positioned inside the aviary enclosures. Alternatively, some sort of tethered run system could be used, although there would be more potential for disaster if the apparatus failed. Such apparatus would fulfil the known requirements for effective learning; the animal is real (i.e. not a model) and it can move with the birds (i.e. predator behaviour both establishes non-predictability and a behavioural contingency). The link between the performance of behaviour (e.g. antipredator response) and the appropriate consequences (e.g. escaping predation) is generally lacking in training exercises that use model predators. This contingency is an integral characteristic of interactions between a wild animal and its environment, but one that is frequently lost in captivity (Shepherdson 1994). The kinds of stressful situations that animals face in

the wild are nearly always those for which an appropriate behavioural response exists. For example when faced by a predator, a wild animal will usually be able to perform an appropriate predator avoidance behaviour. A contingency situation could be established by using non-contact model presentations which allow the birds to move further from the model. If the black stilt juveniles can move away from the perceived source of danger (i.e. the predator), then the decrease in stress may be reinforcing, and the learning of fear of the predator increased. The degree to which the predator animal could "follow" the birds' retreat would be dependent on the extent of the system of tubes. A single system of tubes running through all enclosures of an aviary would enable managers to train all juveniles at once, and birds would be able to see neighbouring birds' responses to the predator. To make the stimulus even more potent, it would be relatively easy to include playbacks of alarm calls during predator presentations (Hill 1986).

The logistic complications of such a technique include designing the tube or tethering system, and training a predator animal to behave appropriately (e.g., not run to a corner and stay there, and one that will allow itself to be put into, and taken out of, the Training equipment). The feasibility of using a wild predator animal can only be assessed by experience. If a wild predator was not practical, a slightly tamed animal, or a realistic motorized model, would be preferable.

3.6.3 Post-release predator training.

Perhaps antipredator-training of captive-reared black stilts while they are in an unnatural captive environment is not optimal. For example, if changing context affects habituation, perhaps context change affects learning more than we are aware, and therefore predator recognition skills acquired in captivity may be forgotten after release. Data from other studies (Beck et al. 1994) has shown only a short term advantage of a costly and labour intensive pre-release training programme to prepare animals before reintroduction. Instead of training while still in captivity, the researchers now train the animals after release and provide them with food, water and shelter so that they can gradually adapt to their new environment and learn survival skills. Perhaps black stilt juveniles would benefit from training after reintroduction. Reintroduced black stilts stay in groups around the rearing aviary complex immediately after they are released from captivity (Adams, work in progress).

Released black stilts that remain in the predator fenced aviary area are able to feed and roost in relative safety. During the time when the black stilts are still in the aviary area it may be both most efficient and most effective to train predator recognition. Presentation of the predator stimulus (i.e. live predator or realistic moving predator model) could occur when a number of birds are near to the presentation area, and could be paired with multispecific alarms calls to increase stimulus potency. Playback alarm calls may not be necessary as a number of birds of other species (pukeko, ducks, spur-winged plover, South Island pied oyster catcher, dotterel, pied stilt) will also be present in the area (pers. obs.) and these birds should respond with natural alarm calls.

Benefits of post-release training are: presentation of the live predator or model would be realistic and surprising; the predator stimulus could approach the birds (live predator could be tethered or trained, and the realistic model directed); presentation time of day and site could vary; different species of predator stimulus could be used (e.g., ferret, stoat); and training would occur at a time of predicted high learning (approximately 8 mths). Disadvantages of post-release training include logistic difficulties and a need for some investment of time and skill. When using a live predator animal it is difficult to always make it behave in the way desired and there is always the risk of the predator escaping (and potentially injuring the birds). The problems of control and risk can be avoided by using a realistic predator model. Design of a realistic model would probably involve some sort of radio controlled system.

3.6.4 Use of other species as surrogate parents in captivity.

The preceding suggestions consider how a model can be used as the conditioning stimulus for antipredator-training of captive-reared black stilts. An alternative method of improving the captive environment for black stilts destined for reintroduction involves using birds of other species as surrogate parents. Providing juveniles with a live parent model could solve a number of general problems associated with hand-rearing birds in captivity. Imprinting theory implies that if black stilt chicks were taken from the incubator and placed under a brooding bird, they would imprint upon that bird as their parent (Lorenz 1970). Having imprinted, juveniles could learn skills

from the bird (e.g. how to preen and what to be wary of).

A mammalian predator could be introduced into a neighbouring aviary (or a model predator into the same enclosure) at critical times in the development of the black stilt juveniles (i.e. prior to fledging and release), and the juveniles could learn from the fear of surrogate "parent". Prior experience with black stilt cross-fostering and sexual imprinting with pied stilts (Reed et al. 1993) suggests that the surrogate parent bird would need to be a species quite dissimilar to stilts. For example, bantams may be appropriate parent models; they are easy to maintain in captivity and are happy to accept and care for eggs and young that are not their own. Additionally, bantams have good recognition of predators and are different enough from black stilts for sexual imprinting to be unlikely.

The disadvantages of the surrogate parent idea include the potential disease risk posed by housing bantams with black stilts, and the possibility that black stilt juveniles may have dysfunctional learning of other skills. Although black stilts are unlikely to sexually imprint on bantams, being reared by a bantam may negatively affect appropriate sexual imprinting on other black stilts in the future (using black bantams may lessen this risk). If black stilt juveniles learn other skills from their parents (e.g. foraging techniques), then a non-wading bird parent (i.e. a bantam) may confuse, or inhibit appropriate skill learning in the juveniles. Testing the importance of potential problems inherent in this suggestion would be possible using either a closely related species (i.e. pied stilt) or very small numbers of black stilts.

3.6.5 Extending the methodology used in this study

Finally, I would like to briefly consider how the antipredator-training technique used in this study compares to the above suggestions. I found that in certain circumstances, antipredator-training (using a predator model moving along a rail accompanied by alarm calls) could produce increased wariness in young black stilts that are raised in captivity. The methodology of this study could be inexpensively extended for larger scale training of entire aviaries (e.g., a longer rail along the entire length of an aviary). However, perhaps the stimulus of a cat model moving on a rail does not provide sufficient realism; and I consider predator realism as an important aspect in any future training regime. Realism may be especially important in species where we know little about their cognitive processing skills. It is currently unknown what cues black stilts

use for recognising mammalian predators; therefore, using as realistic antipredator-training stimuli becomes especially important. For example, perhaps black stilts use movement of animals as a major cue for predator recognition; and it is difficult for models to replicate characteristic mammalian predator movement patterns. My methodology was limited by the constraints associated with designing an experiment (i.e. the need for consistency of stimuli presentation made using models a convenient option) and working within an existing management programme. Such constraints are not present when using antipredator-training for the management of a species. And when considering implementing antipredator-training in the future it would be advisable to attempt to use the strongest, most realistic and most noxious training events permitted.

3.7 The ability of black stilts to generalize antipredator-training

Young animals are known to generalize experience gained in one context to another (Bateson 1982). The ability to generalize is advantageous to the animal, and for species managers. For example, if a black stilt is able to recognize a cat as dangerous, and generalizes this fear to ferrets and stoats (which have many visual cues in common with cats, i.e. four-legs and fur), the ability to generalize may aid in that bird's survival. By training captive-reared black stilt juveniles to fear cats, I expected trained predator recognition to generalize to other mammalian predators, although the validity of this assumption has not been tested. The potential for black stilts to generalize predator recognition requires investigation, and any findings would add useful information to any future species-specific antipredator-training programme. The often extremely human altered state of the black stilts' wild environment (i.e. encroachment of weed species into previously open and braided riverbeds) currently means that an ability to recognise a number of mammalian predators may still not guarantee the survival of reintroduced birds in a predator rich environment. Antipredator-training may give released black stilt juveniles a greater chance of survival than they would otherwise have; and this chance, combined with existing programmes to eradicate weed species from some areas of the Mackenzie Basin (by Project River Recovery) and control predators (by DoC) may provide the advantage black stilts released from captivity require to survive, and ultimately reproduce.

3.8 Summary of recommendations

Having worked closely with the Black Stilt Recovery programme, I am aware that some of my suggestions will be difficult to accept and implement. However, the information gained from this study and the general concepts (if not exact details) could be successfully integrated into the black stilt reintroduction programme. A summary of my suggestions are contained in Table XI.

Table XI. Recommended possible techniques to increase predator wariness of reintroduced captive-reared juvenile black stilts.

DESCRIPTION OF TECHNIQUE	BENEFITS[1]	DRAWBACKS
Contact antipredator training: direct predator/prey confrontations.	Strong stimulus Realistic predation event c=low l=low s=low	Too stressful Ethically questionable
Non-contact antipredator-training: non-contact predator/prey interaction.	Realistic predator Behavioural contingency No harm to the birds l=medium s=medium	Difficult to implement c=high initially
Post-release antipredator-training: live/model predators presented in wild setting.	Surprising stimulus Realistic presentation Variable presentation c=low/medium l=medium s=medium	Logistically difficult Birds may leave the area making training impractical Potential problems with live predator animals
Surrogate parent: learning fear of predators from a "parent".	Teach many skills Respond to all predators Easy to maintain c=low l=low s=low	Inappropriate imprinting Other skills may suffer Disease risk
Moving model antipredator-training: i.e. methodology used in this study	Previously tested Existing equipment Train a number of birds at once c=low l=low s=low	May not be the most potent option Does not "threaten" birds Model outside the aviary

[1] c=financial cost; l=labour cost; s=skill necessary.

3.9 Antipredator-training as an important aspect of reintroduction programmes

In order to protect and restore an endangered species, it is important to fully understand the natural history, ecology, and behaviour of the species and its critical requirements. Most endangered species are endangered for more than one reason, therefore multiple management techniques are needed to conserve them. Conventional biological training or wildlife management techniques alone may not be sufficient (Nisbet 1977). Managers of endangered populations are concerned with whether they can intervene in an endangered bird's life cycle and increase the fitness of the population. But few management programmes have the resources to investigate potential methods of increasing reintroduction success. This study illustrates the important growing role of scientific study in assisting species recovery and management. Regardless of whether behaviour is inherited, learned, or some combination of the two, maintaining animals away from their natural environment for extended periods may, at least potentially, cause qualitative or quantitative differences in components of the animal's behavioural repertoire (Martin & Bateson 1986).

A species that can adapt to a changing environment by altering a traditionally-fixed trait has a greater chance of enhancing its fitness and surviving in a new environment. To enable released animals to cope more effectively once in the wild, captive-rearing programmes currently employ various methods of pre-release training. Pre-release training efforts include: enabling golden lion tamarins to search for hidden and spatially distributed food and to move around on natural vegetation in their cage (Beck et al. 1991); allowing black-footed ferrets (*Mustela nigripes*) to search for and capture live prey in large outdoor enclosures (Oakleaf et al. cited in Beck et al. 1994); encouraging thick-billed parrots (*Rhynchopsitta pachyrhyncha*) to handle pine cones (a primary food source) and fly in pre-release cages (Wiley et al. 1992 cited in Beck et al. 1994); providing natural ponds and vegetation to encourage natural foraging in black stilts (Reed et al. 1993; Sanders & Maloney 1994); and providing opportunities for observational learning about predators in takahe (*Porphyrio mantelli*, Hölzer work in progress). Antipredator-training is just one of the efforts to prepare captive-reared species for life in the wild. Recognition and avoidance of predators is vital for the survival of individual birds in the wild environment, yet little is known about how birds acquire information about predators. Preparing animals for predators that they

will encounter after reintroduction is often perceived as difficult to design and implement, because of the small knowledge base. However, antipredator-training provides the opportunity for captive animals to learn about predators prior to release. Developing effective training techniques requires time-consuming testing and detailed knowledge of the trainee species' behavioural ecology.

Long-term monitoring of the survival of released birds would be required to demonstrate any tangible benefit of antipredator-training. Monitoring of the birds trained in this study does not show that antipredator-training decreased mortality of reintroduced birds (Adams work in progress). However, antipredator-training should only decrease the deaths due to mammalian predators, and the number of animals that have died from suspected mammalian predation are a small proportion of the total deaths (<5%, Adams work in progress). Statistical analyses of mortality statistics were not possible because of the small sample sizes.

Various pre-release training methods have been used to prepare captive-reared animals for reintroduction, with mixed results. Some programmes found a short term advantage (Beck et al. 1994), while findings of others have been encouraging (Ellis et al. 1977). Ellis et al. (1977) found that captive raised masked bobwhites (*Colinus viginianus*) which were exposed to dogs, humans and Harris hawk (*Parabuteo uncinctus*) prior to release, showed greater general mobility, covey coordination, predator avoidance skills, and higher survival rates than inexperienced quail. However, other studies did not show any survival advantage for released animals from using antipredator-training (Miller et al. 1990 with Siberian polecats, *Mustela eversmanni*; McLean & Hölzer unpubl. with New Zealand robins, *Petroica australis*), although in some cases it is too soon to tell (McLean et al. in press, with rufous hare-wallaby, *Lagorchestes hirsutus*). Currently, we do not know if antipredator-training will improve the survival of black stilts. Based on the results of this study, I have suggested that antipredator-training be integrated into the management programme to prepare black stilts for reintroduction. Antipredator-training may heighten black stilt responses to predators in the wild and increase post-release survival.

Rearing species in captivity for reintroduction is becoming increasingly common as a means to rescue species from possible extinction. Currently some captive-rearing programmes are not providing rearing environments which aim to maximise the chances for survival of reintroduced animals (Beck et al. 1994). Intensive captive management programmes are necessarily costly in resources and time. It is important

to remember that labour and money are only *proximate* costs, and counts of surviving birds are merely *proximate* benefits, of investment in the enhancement of captive environments (Biggins et al. 1993). However, time is a luxury some of these species do not have, and the *ultimate* costs of not maximizing survivorship of reintroduced birds could include irretrievable loss of genetic diversity due to mortality of birds, and erosion of survivorship skills due to time spent in a captive environment. I strongly recommend that the preparation for wild environments received by animals raised in captivity include species-specific antipredator-training experiences.

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APPENDIX II

Justification for Methodology Used in this Study

All conditioning experiments can be designed any of a number of different ways (e.g., differences in stimuli type, presentation times and techniques). Deciding on the "nuts and bolts" of the methodology of this study was one of the most time consuming and thought-provoking aspects of the research; and because sample sizes were small, I was able to test few of the myriad of methodological alternatives. In designing the finer details, I found it very difficult to find sufficient detail in the work of others on which to base my methodological decisions. In the interests of aiding future researchers, and answering some questions often posed by critics of this type of work, I have included this appendix to show how the conditioning methodology used in this study was developed; and to provide information on specific areas of the design that may interest future researchers. Some to the information in this Appendix has been mentioned previously in the main text; however, I include it here also to present a comprehensive picture of the background and decision making process involved in this study.

This appendix is divided into sections which combine *Background* information from the literature with the *Requirements* for this study, to arrive at *Decisions* regarding the equipment or stimuli used in this study.

1. General Equipment.

1.1 Screens.

1.1.1 ***Background on the use of screens:*** The influence of watching other animals respond to predators is well known (see main text). For example, when voles (*Microtus arvalis*) were exposed to the sight of a kestrel model, mostly either froze of ran for cover. Neighbouring conspecifics also responded if they were able to see model-exposed voles, but not the kestrel model (Gerkema & Verhulst 1990).

Requirements: It is important for the independence of Test results that birds in neighbouring enclosures can not see the experimental stimulus, or other animals responding to the stimulus.

Decisions: Double thickness hessian screens were used to maintain visual isolation of the enclosures. Each screen was at least 1 m high (higher than the birds), and extended to the ground level.

2. Stimuli Design and Presentation.

2.1 Conditioned stimuli: Models.

*2.1.1 **Background to the model vs live predator debate***: Models are commonly used in behaviour experiments instead of live predators (see Table I; Curio 1975), and especially suitable for the sensitive management requirements of an endangered species. The use of mounted predator models to train endangered species to recognise predators has been successful previously (in rufous hare wallaby, McLean et al. in press; and in takahe, Hölzer work in progress). Magurran & Girling (1986) outline two reasons for not using live animals as training stimuli. Firstly, there is an increasing awareness of the ethical issues raised by predation experiments using live animals (Huntingford 1984). Additionally, it is much easier to replicate the behaviour of a model predator, than to ensure that a live predator behaves in the same way from trial to trial. Issues such as consistency of stimulus presentation may become obsolete when predator training is used as part of a management programme (i.e. out of an experimental context). There are also disadvantages in using model predators: prey animals may not respond to a model as they would to a live predator or, if they do respond, may only perform a limited range of their antipredator behaviours. Second, as with other stimuli, repeated exposure to models may lead to habituation (Manning 1979). Models also differ to live predators because they do not chase and capture prey.

The use of live predator stimuli seems preferable to models because of stimulus realism and some researchers have suggested that live predators could be presented outside the cage, thus posing no danger to the juveniles (e.g., Veltman, pers. comm.). However, juveniles are reared in cages and are potentially aware that a predator outside the cage does not pose them any risk; therefore the strength of training would be compromised, and habituation may occur.

Requirements: The training stimulus needed to be fear provoking, but provide minimum/no risk to the birds. Presentation and behaviour of the stimulus needs to be consistent across trials.

Decision: Models were used instead of a live predator animal.

*2.1.2 **Background to which predator animal would be used***: Black stilts have three mammalian predators (feral cats, ferrets and stoats; Pierce 1980); with the greatest threat to black stilts is thought to be from feral cats because they prey on the birds at all life stages (Pierce 1982). Small numbers of black stilts available for training meant that not all predator animals could be used as training stimuli. If one mammalian predator model is used, evidence suggests that black stilts may be able to generalize recognition of that four-legged, furry predator to others (Bateson 1982).

Requirements: The predator animal chosen for the model used in training should be the one that released black stilts will benefit most from learning to recognize.

Decision: Cats were chosen as the mammalian predator to be represented in this study because: they were considered to be the greatest problem; and they may provide the strongest stimulus (by virtue of their larger size they may provide a "supernormal" stimulus effect; Hamilton & Orians 1965).

2.1.3 Background to details of cat model design and presentation:

(a) Predator models have been extensively used in the past (e.g. scarecrows to reduce crop damage by birds). However, the usefulness of these models has often been limited, as birds normally habituate rapidly to them (Conover 1981); although these same bird species do not habituate to real predators under natural conditions. In the wild environment the spatial context of real predators is always changing, but this is not usually true of predator models (Shalter 1978). If the site of model presentation does not vary there is a danger that juveniles may learn to fear that site, not the predator (Curio 1978, "site-avoidance" hypothesis).

(b) Live predators also differ from predator models because they are animated and most models are not. The most effective predator models have been found to be those capable of movement (Conover 1981).

(c) Sudden movement and moving models (c.f. stationary objects) cause animals to be more fearful than slow moving objects (Nice & ter Pelkwyk 1941). Sudden appearance of models during antipredator-training was used successfully with rufous hare wallaby (McLean et al. in press). Predators are also capable of approaching their prey (i.e. prey can see the face of the predator), studies have found that models that can face prey are more frightening than the same model with its back turned (Strausz 1938 cited in Nice & ter Pelkwyk 1941).

Requirements: The stimulus provided by the model needs to be as realistic as possible by: (a) being variable (i.e. be able to change position) (b) being animated (i.e. capable of movement) and (c) have maximum impact (i.e. be surprising).

Decision: Realism was achieved by using a taxidermist mounted feral cat (trapped in the Mackenzie Basin area). The cat model was mounted with its mouth open and in a walk/low intensity stalk position (Fig. 2 in text).

(a) The stimulus could appear from different positions by altering the position of the box in the cage.

(b) The model was animated by mounting it on a trolley which moved easily along a rail inside the cage (pulled by a system of ropes).

(c) A surprising stimulus was attempted by having the cat model appear from a box inside the cage (Fig. 1 in text, birds had already habituated to the box). Additional model movement was achieved by the ability of the trolley to turn inside the aviary (by using ropes), allowing the model to face the birds.

2.1.4 Background to deciding on an appropriate control model: Choosing a control model is complex because it is difficult to know what stimuli are used by specific animals to recognise objects. Magurran & Girling (1986) found that minnows responded to a realistic model of a pike (realistic markings and shape) as posing the greatest threat, with progressively less life like models eliciting diminished responding. Minnows also habituated more to an unrealistic plain cylinder model than they did to a lifelike marked pike. Therefore, for minnows the shape and colour of the predator stimulus is important in identifying an object as a predator. I consider the black stilts' primarily sensory tool to be their vision and I expect the visual features of a stimulus to be most important (c.f. smell for example). Control models used in other studies vary in their attempts to represent the predator model. For example, Curio et al. 1978 used a multicoloured plastic bottles of similar size and novelty as the animal models used; Maloney & McLean (in press) used a cardboard box of similar dimensions as the predator model and Hölzer (work

in progress) used both a cardboard box and a plastic bottle.

Requirements: The control model needs to control for the movement a novel object (i.e. the predator model on a rail) into the aviary enclosure. The control model must be dissimilar enough from the cat model to make it a valid control. Curio et al. (1978) noted three criteria important in the choice of control models: the control model must be novel; it should be as dissimilar as possible to any predator that may be recognised innately (i.e. without prior experience) and the control model must have a body sized realistically similar to the predator model.

Decision: I decided on a control object made of varnished papier-mâché (Fig. 2 in text). The control was approximately the same height, width and length as the cat model; and mounted on the same trolley-type as the predator model.

*2.1.5 **Background on whether to use a conspecific model during training**:* When training animals to recognize an animal as dangerous, some researchers have found that having "trainee" animals witness a "training" conspecific respond to/or be attacked by a predator aids in learning (Mineka & Cook 1993). Similarly, others have found that using prey and predator animals in a "simulated predation event" increases learning about the predator. For example, Conover & Perito (1981) found that starlings were more wary of an owl model holding a live starling, than they were of either the owl model or tethered starling when presented alone. Also the starlings were more wary of the owl model itself after they viewed it holding a live starling than they were before. However, not all studies have found that using conspecifics reacting to predators is useful in training animals to recognize predators (Bondreau 1968; Maloney 1991).

When using conspecifics in training, the behavioural ecology the animal must be taken into account. Some animals are territorial, and an unknown conspecific (live or model) appearing in their territory may evoke a strong territorial reaction. Black stilt juveniles are reared in aviary enclosures and frequently have "border disputes" with birds in neighbouring enclosures (Reed 1986; pers. obs.); therefore I consider that captive-reared juveniles display territorial behaviour and are likely to respond to a conspecific in their enclosure as an intruder.

Requirements: The Training stimulus needs to relatively easy to operate, and direct the birds' attention towards the predator model as dangerous.

Decision: I decided against using a conspecific model during antipredator-training because I considered that the possible benefits of using the model (e.g., social and observational learning) were not sufficient to outweigh the possible negative effects of such a methodology (e.g., territorial behaviour towards the conspecific model distracting from concentration on the predator model and making the apparatus more complicated, hence more chance for mistakes/malfunctions).

2.2 Unconditioned stimulus: Alarm calls.

*2.2.1 **Background to using alarm calls as an unconditioned stimulus (US)**:* Many parent birds respond to the approach of potential predators by giving alarm calls or distraction displays. Vertebrate "alarm" signals are considered here as signals emitted in the presence of potential predators (Leger and Nelson 1982).

True alarm sounds appear to be innate; and many species respond equally well to either acoustic or visual alarm stimuli (Boudreau 1968). Peeke and Zeiner (1970) reported that habituation proceeds more slowly in rats when the habituation stimulus is a rat distress cry than when it is a tone. This study provides evidence to support the idea that habituation is slower to evolutionary important characters; that is the stilts have a unlearned response to alarm calls that is difficult to extinguish. Antipredator-training techniques common use alarm calls as part of the training stimulus (see Table I in text; Seyfarth & Cheney 1986; Maloney & McLean in press).

Prior to beginning any antipredator-training, I conducted a pilot study that examined the responses of captive-reared black stilts to different sound stimuli. I presented the birds with recordings of silence, white noise, human speech or black stilt alarm calls. I found playbacks of the latter stimuli caused substantially greater alarm in the birds. Similar effects have been found by other researchers (Chandler & Rose 1988; Weary & Kramer 1995). For example, Weary & Kramer (1995) found that eastern chipmunks (*Tamias striatus*) were more likely to flee the area in response to playback of conspecific alarm calls than they were in response to two types of control (silence and white-noise). Chipmunks did not differ in their response to calls recorded from different individuals or calls played back at different amplitudes. Visual and auditory disturbances during playback of calls resulted in a higher probability of fleeing and longer alert times than did the same disturbances in the absence of calls.

Ringtailed lemurs (*Lemur catta*) responded to playbacks of their antipredator calls as they did when the stimuli that elicited those calls were present. (Macedonia 1990). Chandler & Rose (1988) found that the presence of an auditory stimulus dramatically increased the probability of an predator being detected by potential mobbers; and the visual stimulus provides a focus for antipredator responses.

Usually, sounds with sharp onset time (shot gun blast) elicit escape behaviour better than sounds with slow onset time (e.g. approaching aeroplane; Boudreau 1968).

The unconditioned stimulus did not need to be auditory, but designing noxious physical stimuli proved logistically and ethically too difficult. Using auditory stimuli has the disadvantage of potentially effecting "non-target" birds (those not being Trained at that time). However, all experiments were similarly confounded, making comparisons of responses across different types of playback experiments should still be valid (Seyfarth & Cheney 1990). I conducted a pilot study of the number and type of alarm calls heard in the aviary complex over the course of a day (0800 to 2000 hrs). The findings of the pilot study showed that the presentation of alarm calls for the unconditioned stimulus in this study contributed <10% of the total amount (i.e. frequency and duration) of alarm calls heard during a day.

Requirements: The unconditioned stimulus needs to be noxious, and evoke a large alarm response in the birds.

Decision: I decided to use alarm calls as the unconditioned stimulus, with a sharp onset time.

2.2.2 Background to the calls used in this study: (a) The type of alarm call given by black stilts for ground disturbances/predators depends primarily on distance and risk (Reed in prep.). Differing classes of predator sometimes pose

equivalent risks and elicit equivalent behaviour from the prey animal. For example, the response of the American avocet and the black-winged stilt to humans to be much like that to other terrestrial predators (Sordahl 1980).
(b) The alarm reaction of birds to enemies has a biological function and the "alarm" notes are understood by birds of many other species (Nice and ter Pelkwyk 1941). The area around the black stilt rearing aviaries provides habitat for a number of bird species (e.g. banded dotterel, South Island pied oystercatcher, pied and hybrid stilts, pukeko, spur-winged plover, and various species of ducks). In cross-species tutoring experiments, using mobbing calls of other species can bring about the same level of conditioned model recognition as calls of conspecifics (Veith et al. 1980).
(c) Sounds from captive birds are generally not as effective as those make in the field; this may be attributed to both the absence of natural background sounds and the presence of unnatural conditions with affected the caged birds' responses (Boudreau 1968). However, pure and concentrated sound stimuli may elicit "supernormal" responses from birds, similar to the responses of various insects to chemicals (Boudreau 1968).

Requirements: The calls used as an unconditioned stimulus need to reliably elicit alarmed reactions in the juveniles black stilts.

Decision: (a) Experiment I - I recorded some especially clear and noxious alarm calls from captive conspecifics and used these calls for the entire field season.
(b) Results of the first experiment showed some possible habituation to the alarm calls. Therefore, I considered it necessary to use more varied calls for the second experiment. I recorded multispecific alarm calls in response to human intrusion into a nesting area in the wild.
(c) Calls chosen for playback were clear recordings that were relatively free from background noise.

3. Collecting Data.

3.1 Observation of experiments.

*3.1.1 **Background on how experiments were observed**:* (a) Captive black stilts are accustomed to vehicles driving around the rearing compound.
(b) Although the birds seem to be aware of the vehicles, the birds quickly (i.e. <2mins) resume pre-disturbance levels of behaviour (pers. obs.). Hamilton (1975) during his extensive examination of the comparative behaviour of the American avocet and the black-necked stilt used his automobile as a blind while making behavioural observations.
(c) The weather in the Mackenzie Basin is often very hot and very windy in the summer; and extremely cold and frost prone in the winter.

Requirements: (a) The birds should not be aware of the presence of the observer during experimental trials; therefore the observers need to be able to enter and exit the hide unseen. Whilst behind the hide, the observers require enough room and flexibility to operate the video camera, control the experimental apparatus, and have a good view of the birds.

(b) For Testing and Training conducted in the large enclosure, after the car stopped behind the screen, 15 minutes was allowed for the birds' behaviour to return to baseline ("settling" period).
(c) All apparatus must be cheap to construct, resistant to the elements (all year round) and easy to erect and transport; and it would be advantageous to have a hide that blended with the environment.

Decision: (a) The observers approached and left the hide in a small white car.
(b) I constructed hides of double layers of natural brown hessian cloth (cheap, and blends with the environment). The hessian was attached to a number of 2m poles (stable and relatively resistant to environmental conditions).

3.2 How will I measure response?

*3.2.1 **Background to data collection***: (a) Unintentional bias is possible when the observer is transcribing behavioural responses. Some bias can be avoided by using "blind" techniques where ever possible (Kroodsma 1986). "Blind" collection of data occurs when important details of an experiment are unavailable to the observer (e.g., treatments and subjects are unknown).
(b) Because conditioned fear is not observable, it is studied through a change in behavioural responding, which is taken as an index of fear. The primary assumption is that correlation exists between the magnitude of these measurable responses and fear; there is no assurance that this relationship is linear (McAllister & McAllister 1965).

Behaviours are often recorded using a time-sampling technique; time-sampling can be characterized as the systematic recording of a delimited unit of behaviour described in terms of action over a stated time interval which yields quantitative scores by means of repeated time units (Tyler 1979). The relative merits of different sampling methods are mentioned briefly below (see Tyler 1979 for more detail):

PRESENCE/ABSENCE SAMPLING involves the observer recording the occurrence or non-occurrence of a particular behaviour over a time interval. The behaviour is scored once irrespective of the number of onsets within the interval or the amount of the interval that the behaviour occupied. The final score used in presence/absence sampling is the total number of intervals in which the behaviour has occurred. One-zero convention has suffered a great amount of criticism. Altmann (1974) argues that one-zero sampling confuses frequency and duration and gives a poor estimate of both (generally underestimates). Smith & Connolly (1972) point out, where the time interval is small in discontinuous sampling with respect to average bout length, one-zero sampling approximates to instantaneous sampling. In studies where groups are compared and the time interval used is small, apparent differences may still be valid (Tyler 1979).

INSTANTANEOUS SAMPLING occurs where the observer records an individual's current activity at the end of each time interval and is best suited to behaviours which can be easily and quickly distinguished (Altmann 1974).

ALL OCCURRENCE SAMPLING/EVENT SAMPLING involves the observer recording all occurrences of target behaviour produced by a focal individual within a given individual time period. This sampling method is comprehensive and is generally the favoured sampling method (Tyler 1979).

Requirements: (a) All attempts should be made to keep data free from unintentional

bias. (b) The observer should recorded observations which accurately represent the behaviour and motivation (i.e. fear or no fear) of the birds.

Decisions: (a) All data were transcribed from the video-tape "blind" and sampled using small time unit (10s). (b) All attempts were made to record behaviours of importance using the appropriate sampling technique (Table III in text).

3.3 Development and use of a Composite Score.

3.3.1 Background for the development of a Composite Agitation Score for use during Testing: When an animal recognises detects a potential predator it may: ignore the predator and not alter its behaviour; perform overtly defensive behaviour (e.g. fleeing or hiding); attack the predator (e.g. mobbing); or it may perform behaviour patterns that differ from its normal, undisturbed behaviour (Smith and Smith 1989). Behavioural responding depends on recognition of the predator, but not all behaviours overtly demonstrate predator recognition. Different intensities of response often appear in the antipredator behaviours of some animals. In some cases variation in response behaviour reflects differences in the recognition of a predator animal as dangerous; but sometimes the behaviour may really indicate a differing perception of the risk posed by the predator. For example, Columbian ground squirrels (*Spermophilus columbianus*) close to a badger model always ran, whereas those farther away were more likely to remain stationary. When distant from a badger, squirrels are in less imminent danger and may avoid attracting attention to themselves by remaining stationary, whereas the best option for individuals close to the badger may be to flee (MacWhirter 1992).

Other features of behaviour make measuring intensity of antipredator recognition and response difficult; and example of a confounding factor in motivation measurement is the displacement activity. A displacement activity is the performance of a behaviour pattern out of the context that the behaviour would usually be related (Thorpe 1963); and often seems to occur without the normal eliciting stimuli (Marler & Hamilton 1966). Displacement activities often involve the performance of behaviours that do not seem to be appropriate for the situation (e.g. birds displacement feeding and preening in the presence of predators (Simmons & Crowe 1953). Displacement activities include sleeping (Simmons & Crowe 1953), feeding and preening (Simmons 1955; Hamilton 1975). Reliably identifying the motivation behind certain behaviours is complicated by the occurrence of displacement behaviours. For example, does a high frequency of feeding in the presence of a predator imply that the bird does not recognise the predator as dangerous, or is the bird investing in a displacement behaviour and is actually very aware of the dangers in the situation?

The range of responses an animal may give to a predator animal has been coped with by some researchers by developing compound measures of overall response (Robertson & Norman 1976; Giles & Huntingford 1984; Maloney 1991). When developing a compound measure of behaviour, it is important to decide which behaviours will be positively loaded (i.e. a high score indicates a behaviour that is perceived to a indicate a positive antipredator response) or negatively loaded (i.e. performance of such behaviours are not considered to indicate predator wariness). The loading of specific behaviours was provided from personal observations and the literature on antipredator responses of black stilts and related members of the Recurvirostridae family (all behaviours

described in Table III):

Positive loadings -

STEPPING: High step rate indicates medium/high intensity antipredator reaction (Simmons 1955; Sordahl 1980;). Normal undisturbed behaviour is usually associated with a medium step rate (i.e. the birds are often moving around feeding pers. obs.). A very low step rate usually indicates alertness (i.e. the birds are stationary and watching a disturbance, pers. obs.) or that the birds are resting.

HEAD BOBS: An alert or low intensity alarm response, frequently performed when the bird is disturbed (Simmons 1955; Hamilton 1975; Marchant & Higgins 1993).

UPRIGHT POSTURES: Associated with alertness and "suspiciousness"; the elongation of the neck in this behaviour may allow the wader to get a better view of the danger (Simmons 1955). A low intensity alarm response (Simmons 1955; Hamilton 1975; Reed 1986).

FORWARD POSTURES: Often used in intraspecific interactions as a threat behaviour; but does occur in predator reactions (Simmons 1955). Thought to be of similar/slightly greater intensity as upright postures (pers. obs.).

HOPS AND FLAPS: Performed often by disturbed resting birds, or just prior to flying (Hamilton 1975). Usually considered a medium intensity alarm reaction (Simmons 1955).

FLIGHTS: Flying is a high intensity escape/alarm behaviour (Simmons 1955) and is common in the presence of predators (Sordahl 1980).

ALARM CALLS: Occur in response to disturbance (Simmons 1955; Reed 1986; pers. obs.) and especially to potential predators (e.g. humans, dogs) (Sordahl 1980; Reed 1986).

DISTANCE: Animals maintain larger distances from predators when aware of risk (Conover & Perito 1981; Giles & Huntingford 1984)

Negative loadings -

FORAGING: Foraging behaviour has been found to decrease in other animals in response to predator models (Mollenauer et al. 1974; Conover & Perito 1981; Giles & Huntingford 1984; Magurran 1986)

PREENING: Preening is a maintenance and nondefensive behaviour (Simmons 1955; Hamilton 1975; Reed 1986) and has been found to decrease in animals in the presence of predators (Mollenauer et al. 1974).

RESTING: Resting is a nondefensive behaviour and has been found to decrease in the presence of predators (Mollenauer et al. 1974).

Behaviours of uncertain/neutral motivation -

RUN AND FREEZE and HUNCH: These behaviours are relatively rare, and of uncertain motivation and alarm intensity.

COMFORT MOVEMENTS: Comfort movements are those maintenance activities which aid in the animals personal care. There is a possible correlation between disturbance and frequency of performance of certain comfort movements (e.g. two-winged stretch, wing and leg stretch, yawning, feather movements; Hamilton 1975); however the strength and reliability of such a correlation is uncertain.

SUBSTRATE and COVER: Little or no useful information could be found to contribute to a possible loading for these factors.

HEAD TILT: Tilting of the head is a common response to aerial disturbance (e.g. overflying birds of different species, aeroplane; Marchant & Higgins 1993; pers. obs.).

HEAD ORIENTATION: Keeping a potential predator in sight and under observation is an advantage for prey.

Requirements: The Composite Agitation Score must attempt to represent each birds' overall motivation (i.e. intensity of fear due to the stimuli) as accurately as possible. Scores should be positively correlated with fear.

Decision: The scoring of behaviours is shown in text (Table IV). The "quantity" of behaviour associated with each Score was allocated *a priori*, and relatively arbitrarily, by combining aspects of the literature with personal observation of black stilts. However, important details to note are the non-linear scoring of stepping, resting and preening. STEPPING: I reasoned that both very low and high stepping rates indicate agitation in black stilt juveniles. A medium stepping rate is associated with normal feeding and locomotion in the enclosure; I therefore allocated Composite Scores that reflected the intensity of the response (i.e. higher scores indicate higher agitation). RESTING: I considered that resting in the presence of the predator model reflected a very low wariness response; therefore, I assigned the presence of this behaviour the lowest Score possible and the opposite behaviour (i.e. not resting) the highest Score possible. PREENING: I had similar reasons for allocation of Scores for preening as for resting. Although, I believed that preening does not indicate a wariness response as low as that of resting, because the bird can still be roused to flight quickly and can keep the predator under surveillance whilst preening. Therefore, I gave preening the lowest possible Score, and not preening a medium Score.

3.3.2 ***Background for the development of an Intensity of Training Response Score***: Researchers have found that learned response correlates strongly with the response during learning (Veith et al. 1980).

The most important antipredator strategy of young avocets and stilts is to seek cover and hide, or simply crouch in the open as soon as danger threatens

("freeze"), and then depend on the aggressive and/or diversionary behaviour of their parents (Sordahl 1980; Pierce 1982). As chicks age the "freeze" behaviour declines and running becomes the common escape response (Hamilton 1975). After fledging the most extreme antipredator response is flight (Sordahl 1980). For example, a typical stilt response to a mammal predator was witnessed by Sordahl (1980), and consisted of the birds making one or two very loose swoops or circled the mammal, then landing 5-10 m from the predator, and walking about in the upright posture, calling and head bobbing.

Requirements: The Training Response Intensity Score (TRIS) should reflect the intensity of the alarm response during antipredator-training.

Decision: The scoring of behaviours is shown in text (Table V); with high intensity alarm behaviours given high scores.

4. Maximumizing Learning and Minimizing Habituation

4.1 General conditioning considerations

4.1.1 Background to how conditioning works with respect to antipredator-training: An "unpleasant" experience with an enemy will intensify the reaction, while indifferent experience will weaken the reaction (Nice & ter Pelkwyk 1941). For example, a noxious experience with a predator model may condition black stilt juveniles to react with more wariness to the model; whereas a benign experience with the predator model (i.e. as in Pre- and Post-Tests) may weaken the reaction.

(c) Rachlin (1976) contends that temporal contiguity is the key to learned behaviour. When two events occur at the same time, or in quick succession, they become associated. The more there are of these contiguous occurrences, the stronger the association. Another relation between the CS and US, that governs the rate of classical conditioning, is the relevance between CS and US. The idea is that the US has to be surprising to produce learning. Presumably learning occurs rapidly during the first few pairings of the CS and US because during these initial conditioning trials the US is not yet predicted by the CS and is therefore still surprising (Domjan & Burkhard, 1986). Miller (1951) assumes that fear has motivational properties and that it energises behaviour and its reduction serves as a reinforcer. Therefore, if the alarm calls, and subsequently the cat, are considered to be noxious then the withdrawal of these stimuli should prove reinforcing. The implications for this study of such an assumption is that the training should be short, so the withdrawal of the noxious stimuli reinforces the appropriate startle/escape response, not the inquisitory approach response that would occur if the training was permitted to last for longer. Similarly, the extinction of training that may occur with testing would be significantly less if testing presentations of the cat were shorter.

(d) One usually thinks of repetition as a basis for habituation, but within limits it is informative and can augment responses. For example, a 30 second playback of warning calls elicited many more post-stimulus responses from fowl than did bouts that were only 10 seconds long (Shalter, 1974). Similarly, Beer (1973) discovered that repetition of a signal was a crucial feature in eliciting alarm responses from captive Laughing Gull chicks.

Decision: (a) This idea has two implications, firstly that there is a need to keep the CS/US pairings few so as to retain stimulus potency. And, secondly, the CS should predict the US (ie. the cat should appear just before the alarm calls), this is opposite to the 1992/93 regime where it was considered most important to imitate the natural occurrence of alarm calls and cat appearance. Current research suggests that during conditioning the organism attempts to detect the causal structure of its environment and the CRs generally occur to the most reliable predictor of the occurrence of the US. In the absence of a reliable predictor, conditioning may not occur (Mineka & Cook, 1993).
(b) The US will be as powerful and surprising as possible. This means that the calls will not all be the same (call novelty), they will not always come from the same place (spatial novelty) and they will be loud and noxious to the birds (not necessarily appropriate).
(c) For each training event the cat (CS) will emerge slightly before the alarm calls (US) begin, and this will be repeated so the CS is perceived to be predictive of the US. Although each training event will be relatively short (approx 30 seconds) so as to avoid habituation to the stimuli.
(d) The length of the training event will be relatively short (<30 seconds) so the birds do not cease to pay attention to the stimuli, grow used to the cat, or possibly have inappropriate behaviours reinforced (such as approach behaviours due to loss of initial fright of stimuli) by the withdrawal of the cat and the termination of the calls.

4.2 Testing of Responses

4.2.1 ***Background about why Testing black stilt responses was a necessary part of the experimental design:*** To quantify the change in an animal's antipredator response due to Training it is necessary to compare the baseline response level (i.e. Pre-Test) to the response level after Training. This experimental design contributes power to the analyses because each animal acts as its own control. Such before/after testing regimes have been used in other antipredator training experiments (Maloney & McLean in press; McLean et al. in press). Testing usually involves presenting the Test model (i.e. the cat or control models in this study) for a fixed period. The period of model exposure is usually determined by making a compromise between the length of time necessary to record a response, and the time before habituation is thought to occur. Test duration in previous studies has varied from 5 minutes (Maloney & McLean in press) to 90 minutes (McLean et al. in press). Using a video-camera to record juveniles' responding during experiments may decrease the length of the Test necessary to collect detailed data on recognition response.

Requirements: Test duration needed to be long enough for sufficient data on recognition to be collected, but not so long that habituation occurs.

Decision: I considered that black stilt juveniles would begin to habituate to test models after a period of less than five minutes; and because of the amount of detail it was possible to record from the video-tape, I considered that Testing should be kept as short as possible. Experiment I: I decided on a Test duration equivalent to the length of a Training session (220s). However, habituation seemed to occur in the first experiment, so I lessened the duration of Tests to 3 minutes (180s) for Tests at ages that accompany Training (i.e. 1

mth, 6 mth and 9 mth), and 2 minutes (120s) for the Recognition Test when the birds are 2 mths old.

4.3 Best Training Times.

***4.3.1 Background on appropriate ages to antipredator train black stilt juveniles*:** There is nothing known about the critical period for learning in juvenile black stilts; but considering the long semi-dependence period of these animals (they remain with their parents for 50% longer than their pied relative), I expected there to be a protracted period for learning, rather than a small critical window. The effects of parental behaviour on offspring fitness are likely to be strongest in species with extensive parental care (Cully & Ligon 1976; Stamps 1991).

Perhaps the best time to learn about predators would be during the fledgling stage. During this 1 month period chicks observe their parents' reactions to scores of predators and non-predators each day (Sordahl 1980).

During winter and early spring, food is scarce for predators, and predators are almost breeding and need to find food for their young. This time of food scarcity corresponds with black stilt juveniles being approximately 6 mths old.

Juveniles often remain with their parents up to the age of 9 mths, then leave the family group for full independence in the wild (Pierce 1982).

Requirements: Antipredator-training should take place at times in black stilt development where greatest adjustment in behaviour is likely to occur. Training sessions should take into account the time constraints of the observer and existing management programme.

Decisions: Experiment I: Training occurred for all birds immediately after fledging (40-50 d), and for some birds at additional ages (Table VI in text; timing of second training due to observer time constraints). Experiment II: Training of all birds occurred at three ages. The three ages were prior to fledging (<30 d), and at 6 and 8 mths.

***4.3.2 Background on how long and frequent antipredator-training should be*:** Some researchers have found that repeated presentations of stimuli are necessary for learning of responses to occur (Beer 1973; Boudreau 1968; Shalter 1975). Mineka & Cook (1993) found indications that the level of acquired fear in a rhesus monkeys that reared one sessions of observation training of snakes was less robust and less well maintained then those that were trained for two sessions. Although both the one and two session groups showed acquired fear of snakes at post-test, at follow-up, the two-session observers continued to show a fear of snakes, but the one-session observers did not. Mineka and Cook (1993) study results suggest that learning may be asymptotic or close to asymptotic after two sessions of observational conditioning (involving a total of 8 minutes of exposure to the model behaving fearfully with snakes). However, others have found that repeated presentations of stimuli cause habituation (see discussion in text, Chapter 3).

In some circumstances a single aversive experience with a predator is sufficient for animals to learn predator wariness. For example, European minnows learned to be wary of a predator after a simulated predator attack. The experience of the minnows was brief and involved no overt attacks or

kills; nevertheless it produced long-lasting effects (Magurran 1990).

Avoiding habituation is a major aim in the length of stimulation in training events. Habituation rates are highly species specific, and a degree of intelligent guesswork is necessary when deciding on stimuli presentation times. An example of the process of habituation rate is provided by Herzog et al. (1989). This study investigated the habituation of defensive attacks directed toward a threatening stimulus in neonatal garter snakes (*Thamnophis spp*). Newborn garter snakes were given daily tests in which snakes were confronted with a nonmoving and moving human hand. Over five successive test days the neonates showed a decline in number of strikes directed toward the stimuli. When retested 10-13 days later the animals showed significant response recovery. There were large individual differences in habituation rates. Other studies have also found significant individual differences in habituation to a predator model; for example Shalter (1978) found that habituation to stimuli (stuffed owl) required up to 10 presentations of 15 minutes, followed by 15 minute break. House sparrow (*Passer domesticus*) and house finches (*Carpodacus mexicanus*) in flocks began to adjust to gunfire and detonator noise after six consecutive exposures at four-minute intervals, and all had adjusted after about the fifteenth exposure (Boudreau 1968).

Habituation and learning are related to both duration and frequency of stimulus presentation. For example, Hinde (1954, cited in Peeke & Herz) found that habituation of the chaffinch (*Fringilla coelebs*) mobbing response to owls proceeds more rapidly with spaced trials than with massed trials. He reported that 2, 3, 4, or 5 three minute presentations of owl models on successive days resulted in more habituation than did presentation of 20 minutes on each day. This spacing effect has implications for learning trials.

Requirements: Antipredator-training should be long enough to reinforce learning, but not long enough for habituation to occur.

Decisions: I decided to keep the presentation of the training stimulus relatively short. In Experiment I timing was four presentations of 40 s with 20 s breaks between. However, due to the occurrence of habituation I considered that the time of the presentations should be decreased and less frequent in Experiment II (2 presentations of 30 s with 30 s break in between).

I decided on spaced Trainings, but only over the course of one day. The number of Training sessions decreased between Experiment I and II, also in the interests of minimising habituation.

*4.3.4 **Background on what time of day training be***: (a) Cats are active around the hours of darkness (King 1984). (b) The video camera does not record sufficient detail to allow experiments to be conducted at night.

Requirements: (a) I hope to mimic the wild situation as close as possible (although this is not critical). (b) The birds' responses to the stimuli need to be recorded by the video camera. (c) All experimental activity must occur at times convenient for the existing management programme.

Decisions: Experiment I: three training episodes at four hour intervals during the day. Training occurred at morning (approximately 0800), midday (approximately 1200 hrs) and afternoon (approximately 1600hrs). Experiment II: two training episodes per day, one at early morning (approximately 1-3 hrs after sunrise) and the other in late afternoon (approximately 1 hr before sunset); these times approximately correspond to cat activity patterns.

APPENDIX III

Historical and behavioural data for juveniles in Experiments I and II

A) EXPERIMENT I: History of juvenile black stilt subjects, including the difference (Post-Test minus Pre-Test) in the mean distance maintained from the cat model.

CONDITION	BIRD	MEAN (m)	CLUTCH	NO. IN CLUTCH	PARENT[1]	FATE
untrained	wy/yw	-0.41	1	4	A	dead
untrained	wy/wbk	-0.45	1	4	B	dead[2]
untrained	wy/wy	-0.43	1	4	A	dead
untrained	wy/yg	-0.64	1	4	A	alive
untrained	wy/gy	0.00	5	4	B	alive
untrained	wy/gw	-0.07	5	4	B	dead
untrained	wy/gg	-0.02	5	4	B	dead
untrained	wy/gr	0.25	5	4	B	alive
untrained	wy/bkr	-0.36	8	2	G	alive
untrained	wy/bkbk	-0.77	8	2	G	alive
untrained	wg/wr	-0.30	10	3	E	alive
untrained	wg/wg	0.07	10	3	E	alive
untrained	wg/wbk	-0.48	10	3	E	dead
trained	wy/wg	-0.12	2	4	C	dead[2]
trained	wy/rw	0.36	2	4	H	dead
trained	ww/gbk	0.24	2	4	H	alive[3]
trained	wy/ry	0.19	2	4	D	alive[3]
trained	ww/rbk	0.07	3	4	D	dead
trained	ww/wbk	0.00	3	4	D	dead
trained	ww/ybk	0.27	3	3	D	dead
trained	wy/yy	0.25	4	3	E	dead
trained	wy/ybk	0.07	4	3	E	dead

CONDITION	BIRD	MEAN (m)	CLUTCH	NO. IN CLUTCH	PARENT[1]	FATE
trained	wy/gbk	0.27	4	4	E	dead[2]
trained	wy/wr	-0.23	6	4	F	dead[2]
trained	wy/bkw	-0.20	6	4	F	alive
trained	wy/rbk	-0.25	6	4	F	dead
trained	wy/yr	0.07	6	3	F	dead
trained	wy/bky	0.14	7	3	G	alive
trained	wy/bkg	0.34	7	3	D	dead
trained	ww/bkbk	0.14	7	4	G	dead
trained	wg/yg	-0.02	9	4	H	alive
trained	wg/yr	-0.20	9	4	H	dead
trained	wg/yw	-0.05	9	4	H	dead
trained	wg/yy	-0.05	9	4	H	dead

[1] Key to parents: A = by/y x black; B = rb x y/ww; C = mg/b x black; D = mb/y x wg/r; E = bm/y x wg/r; F = yy/g x gw/g; G = gr/g x black; H = gw x node I; I = node H x node I

[2] died in captivity.

[3] retained in captivity.

B) EXPERIMENT II: History of juvenile black stilt subjects

BIRD	BANDS	CLUTCH	NUMBER IN CLUTCH	PARENTS[1]	FATE[2]
1	wbk/rr	1	4	A	retained
2	wbk/yg	1	4	A	retained
3	wbk/rg	1	4	B	retained
4	wbk/ry	1	4	C	alive
5	wbk/yw	2	3	B	dead/other
6	wbk/ww	2	3	B	alive
7	wbk/wbk	2	3	D	dead/other
8	wbk/wg	3	3	E	dead/other
9	wbk/wr	3	3	E	alive
10	wbk/wy	3	3	E	dead/pred.
11	wbk/ybk	4	4	F	dead/other
12	wbk/gg	4	4	F	alive
13	wbk/yr	4	4	F	alive
14	wbk/gw	4	4	F	dead/other
15	wbk/bkw	5	3	G	dead/pred.
16	wbk/gr	5	3	H	alive
17	wbk/gbk	5	3	H	dead/other
18	wbk/bkbk	6	3	I	dead/other[3]
19	wr/ybk	6	3	G	alive
20	wbk/bkr	6	3	G	dead/other[3]
21	yr/bkw	7	3	J	dead/other
22	yr/bky	7	3	G	dead/pred.
23	yr/gg	7	3	J	alive
24	yr/bkr	8	3	H	alive[4]
25	yr/bkbk	8	3	H	alive
26	yr/bkg	8	3	H	alive
27	wr/rw	9	3	K	alive
28	wr/ry	9	3	K	alive
29	wr/rg	9	3	K	alive

[1] Key to parents:

A = black x node I	B = ww/wy x ww/w
C = wy/g x mg (node I)	D = ww/wy x wr/w
E = bm/by x wr/r	F = br/r x black unbanded
G = yg x yr/ww	H = yy/g x node I
I = b- g/wr	J = ww/yr x black

K = Queenstown captive pair

[2] Key to fate:

retained = retained in captivity as breeding stock
alive = sited at least three months after release into the wild.
dead/other = died from human related factors (e.g., powerlines) or of unknown causes.
dead/pred. = died of suspected aerial predation

[3] Birds are still alive, but treated as dead for the analysis because they became injured and required recapture.

[4] Bird was alive at the time of statistical analyses; is now dead due to being hit by a car.

C) Response measures of black stilt subjects: Testing/Training in large aviaries; n=29 for all Tests. CAS=Composite Agitation Score, refer Table IV; TRIS=Training Response Intensity Score, refer Table V.

Bird	Recog. CAS		6 mth CAS			9 mth CAS			TRIS	
	cat	cntrl	Pre-	Post-Tests		Pre-	Post-Tests		6	9
	Test	Test	Test	cat	cntrl	Test	cat	cntrl	mth	mth
1	8	5	16	10	8	9	10	7	6	8
2	7	7	17	7	8	14	7	11	6	8
3	7	5	15	6	9	11	6	7	6	8
4	9	5	15	9	9	12	9	9	6	8
5	9	5	9	10	7	11	10	11	8	6
6	11	6	12	6	6	12	6	5	8	6
7	12	6	11	9	6	10	9	9	8	6
8	16	8	18	13	5	12	13	7	8	8
9	18	9	16	9	4	10	9	6	8	8
10	17	8	16	12	4	11	12	7	8	8
11	8	8	11	10	10	13	10	12	9	8
12	11	9	12	11	9	15	11	9	9	8
13	11	5	13	7	8	13	7	9	9	8
14	11	7	11	8	10	13	8	11	9	8

15	11	7	8	11	5	10	11	14	4	9
16	7	8	10	6	8	10	6	10	4	9
17	7	6	11	10	7	10	10	10	4	9
18	15	8	13	10	6	9	10	7	9	6
19	8	9	9	7	4	9	7	12	9	6
20	12	9	11	6	6	8	6	8	9	6
21	12	8	6	11	13	11	11	10	4	5
22	9	6	6	9	8	9	9	8	4	5
23	12	6	4	10	12	7	10	7	4	5
24	6	5	15	4	7	5	4	5	5	5
25	6	5	14	5	6	7	5	5	5	5
26	6	5	15	5	10	7	5	5	5	5
27	12	5	10	4	8	6	4	10	6	6
28	13	7	10	5	4	6	5	7	6	6
29	12	6	9	6	4	5	6	6	6	6

D) Mean ± standard errors of the difference in Composite measures for the comparison between clutches of different sizes

AGE (mth)	COMPOSITE MEASURE[1]	NUMBER OF INDIVIDUALS IN A CLUTCH		P[2]
		3	4	
		n=21	n=8	
6	CAS	-3.05±0.76	-5.88±0.99	0.036
6	TRIS	6.29±0.43	7.50±0.57	0.071
9	CAS	-0.86±0.43	-4.00±0.87	0.002
9	TRIS	6.42±0.31	8.00±0.00	0.011

[1] CAS = Pre-Test minus cat model Post-Test Composite Agitation Scores (as per Table IV); TRIS = Training Response Intensity Score (as per Table V)

[2] All comparisons are between scores for different clutch sizes using Kruskal-Wallis tests.